THE REPRODUCTIVE AND FORAGING ECOLOGY OF WADING BIRDS (CICONIIFORMES) AT LAKE OKEECHOBEE, FLORIDA

By

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I documented the distribution and abundance of nine species of wading birds at Lake Okeechobee, Florida, from August 1988 through August 1992. The study period spanned a two-year drought. The highest diversity and numbers of foraging birds occurred during peak drought periods, in part indicating that the lake serves as a regional drought refuge. Regulation of lake water levels is a priority management issue. Lake stage set the upper and lower limits to accessible habitat; otherwise, receding water was a strong attractor to foraging birds. Habitat selection analyses indicated a general preference for wet-prairie habitats of intermediate stature and structural diversity, but all species selected prey-rich beds of submerged vegetation at low lake stages.

I documented the history of nesting from 1989-1992 through aerial surveys, studied the nest productivity of six species in select colonies, and documented the foraging habits of nesting adults of four species through aerial following flights. Interior-marsh colony sites were abandoned in favor of island sites during the drought. The

widest variety of sites was used during 1992 with high lake stages, but this usually did not translate to higher nesting success. Great Blue Herons (Ardea herodias) and Great Egrets (Casmerodius albus) initiated more nests in high-water years. Little Blue Herons (Egretta caerulea) initiated the most nests in 1989 following a multi-year period of high water. Snowy Egrets (E. thula), Tricolored Herons (E. tricolor), and White Ibises (Eudocimus albus) initiated the most nests during the peak drought year of 1990 and the fewest in 1991 with moderate but stable water levels. All species achieved high nest success and productivity in 1990 and the lowest levels either in 1991 or in 1992 with high water. Thus, drought-related declines in the lake stage enhanced aspects of all species' nest productivity, but species' responses differed in subtle ways. Logistic regression analyses confirmed a high degree of complexity with regard to the environmental determinants of nest failure. I programmed an energy-circuit population model for Great Egrets to conceptually organize data and further study relationships between environmental forcing functions and the foraging and nesting ecology of one common species.

CHAPTER 1
PROJECT INTRODUCTION

Impetus For the Lake Okeechobee Ecosystem Study

In April 1988, the South Florida Water Management District (SFWMD) formalized a 5.5-year contract with a diverse team of researchers from the University of Florida and the Florida Game and Fresh Water Fish Commission (FGFWFC) to address the task of establishing a comprehensive database on the ecological dynamics of Lake Okeechobee (Aumen 1994). Lake Okeechobee is the third largest freshwater lake within the United States (1,732 km^2 surface area; Herdendorf 1982). It drains a 12,000 km^2 watershed primarily through the Kissimmee River from the northwest, and is in turn the headwaters of the Everglades and Florida Bay to the south. Besides supplying water to the Everglades, the lake is the primary source of water for a burgeoning urban population and for the extensive Everglades Agricultural Area (EAA) situated just south of the lake. It serves as a regional flood-control facility and supports a multi-million dollar commercial and sport fishing industry. It supports a large nesting population of the endangered Snail Kite (Rostrhamus sociabilis; Sykes 1979; Snyder et al. 1989) and a large population of once-endangered but now recovering alligators (Alligator mississippiensis; Mazzotti and Brandt 1994). It also provides important foraging and nesting habitat for most of the species of wading birds that occur in Florida (Zaffke 1984; David 1994a, b; Chapters 2, 4), often including the endangered Wood Stork (Mycteria americana; Browder 1976; Chapter 2). The demands of these diverse interests often conflict, and consequently management of the lake is a subject

of considerable debate. Public concern over the health of the lake peaked in 1986 with the occurrence of unusually massive blue-green algal blooms (Fox 1987). This added to growing frustration over waterways choked with exotic plant species such as Hydrilla verticillata and water hyacinth (Eichhornia crassipes), and the expansion of other nuisance species such as cattail (Typha sp.) and the exotic Melaleuca quinquenervia.

Beginning in 1973, researchers measured phosphorous loading rates in excess of critical values established by Vollenweider (1968) for eutrophic lakes, and recently established that total phosphorous concentrations in the pelagic zone of the lake had doubled since 1973 (see Aumen 1994 for a review). The appearance of previously undocumented, large scale algal blooms and the associated negative side effects--including fish kills, foul odor and taste of lake water, and public outcry--summoned new concern among managers within the SFWMD over the potential relationship between lake eutrophication and the prevalence of algal blooms and other invading plants. The long-term ecological consequences of the proliferating blooms are unknown and the ability to monitor present and future impacts was limited due to a paucity of information on the ecology of the lake. Residents, scientists, state officials, and managers were particularly concerned over the possible negative impact on the trophic structure of the lake. Fish kills related to the toxicity of algal blooms understandably elicited widespread concern and precipitated a call for immediate action to curb inputs of nutrients believed to be contributing to the blooms. Bearing the brunt of criticisms in this regard were the large dairy farms located around the north end of the lake and the sugar cane industry in the EAA. However, without specific and detailed data to support claims, assessing the feasibility and effectiveness of proposed plans of action was at best an uncertain task. Consequently, the SFWMD solicited the participation of university and FGFWFC researchers to establish a baseline ecological dataset on

which future management strategies and additional specific research plans could be based.

I became involved in the ensuing Lake Okeechobee Ecosystem Study as a graduate student, with the responsibility of implementing a comprehensive study of the reproductive and foraging ecology of wading birds at the lake. Other members of the research team were responsible for studying the hydrologic and vegetation dynamics of the ecosystem, water quality and nutrient dynamics, phytoplankton and zooplankton community dynamics, benthic invertebrate communities, and fish community dynamics. Most of this work will be summarized in a special Lake Okeechobee edition of Archiv fur Hydrobiologie, to be published in late 1994 or early 1995. Field work on the project began in May 1988 and ended in December 1992. I began surveying foraging wading birds in August 1988. Following the preliminary 1988 fall survey season, I focused my research efforts on the typical wading bird nesting season, January through August, and completed four seven-month field seasons from 1989-1992. Several of the analyses I subsequently conducted relied on the diverse datasets prepared by my colleagues on the project--specifically the output from a hydrologic model and vegetation maps prepared by J. Richardson and his coworkers, additional vegetation data collected by P. Zimba and his coworkers, and data on prey populations gathered by J. Chick and C. McIvor, and by L. Bull and his coworkers.

Wading Birds in Southern Florida and at Lake Okeechobee

The plight of Lake Okeechobee and the potential threat of large-scale algal blooms has only recently garnered significant attention. However, the decline of wading bird populations in southern Florida has received considerable attention. Early in the century, the plume-hunting trade had a severe impact on regional populations,

but since then ill-advised hydrologic manipulations and habitat degradation have played the major role in nesting population declines as high as 90% since the 1940's (Kushlan and White 1977; Ogden 1978a, 1994; Kushlan et al. 1984; Kushlan 1986a; Kushlan and Frohring 1986; Walters et al. 1992; Bancroft et al. 1994; Frederick and Spalding 1994). Several recent studies have addressed the relationship of habitat availability, hydrology, and wading bird reproductive success in various regions of southern Florida (Kushlan et al. 1975; Kushlan 1976c, 1986a; Browder 1976; Ogden et al. 1978, 1980; Powell 1987; Frederick and Collopy 1989a; Frederick et al. 1992; Frederick and Spalding 1994; Bancroft et al. 1994; Ogden 1994). These and other continuing efforts are building a solid base of information that will provide Florida managers with the knowledge necessary for managing and maintaining healthy wading bird populations in southern Florida. Previously, only general information was available concerning the population dynamics of wading birds at Lake Okeechobee (Zaffke 1984; David 1994a, b), and therefore my work filled an important gap in the regional knowledge base. In particular, I was afforded the opportunity to augment scarce information concerning the ecological dynamics of wading birds in a naturally occurring--albeit highly regulated--southern Florida lacustrine ecosystem.

Wading birds comprise a particularly conspicuous component of the southern Florida fauna. Their colonial breeding habits facilitate the study of their reproductive efforts, and the large size and white color of several of the major species facilitates monitoring populations through aerial surveys. Colonial-nesting wading birds are sensitive to changes in their nesting and foraging habitat (Kerns and Howe 1967; Kushlan 1974, 1976c; Wiese 1978; Ogden et al. 1980; Bancroft et al. 1994; Frederick and Spalding 1994; Ogden 1994). Wading bird distribution, diversity, abundance, and reproductive performance all reflect the characteristics and distribution of available prey

populations (Owen 1960; Dusi and Dusi 1968; Kushlan et al. 1975; Rodgers and Nesbitt 1979; Kushlan 1976b, c, 1978a, 1981, 1986a; Browder 1976; Bancroft et al. 1994; Frederick and Spalding 1994; Ogden 1994). These links to other less conspicuous elements in the food web of ecosystems like Lake Okeechobee, and the high visibility of wading birds, has led many authors to conclude that wading birds are reliable bioindicators of change in hydrological and ecological conditions in wetland ecosystems (e.g., Custer and Osborn 1977; Curry-Lindahl 1978; Hafner and Britton 1983; Bildstein et al. 1990; Kushlan 1986b, 1993; Ogden 1994).

Lake Okeechobee has consistently supported several large, mixed-species wading bird nesting colonies each year (Ogden 1978a; Osborn and Custer 1978; Nesbitt et al. 1982; Zaffke 1984; David 1994a; Chapter 4). The aquatic-feeding species that commonly nest in relatively large numbers include Great Blue Heron (Ardea herodias), Great Egret (Casmerodius albus), Snowy Egret (Egretta thula), Tricolored Heron (E. tricolor), Little Blue Heron (E. caerulea), and White Ibis (Eudocimus albus). Black-crowned Night Herons (Nycticorax nycticorax), Green-backed Herons (Butorides striatus), and Glossy Ibises (Plegadis falcinellus) also nest at the lake in small numbers, and Wood Storks have occasionally nested at or near the lake in the past. The primarily terrestrial-feeding Cattle Egret (Bubulcus ibis) also nests in large numbers at the lake.

The success and productivity of wading bird nesting efforts often depends on favorable hydrologic conditions (Frederick and Spalding 1994). Colonies on Lake Okeechobee and in marshlands typical of the Everglades are usually situated in areas surrounded by water, probably to discourage invasion by mammalian predators (Jenni 1969; Frederick and Collopy 1994). However, the willows that wading birds at Lake Okeechobee generally nest upon are weakened by excessive inundation (Zaffke 1984;

David 1994a), and willow reproduction is dependent on reduced water levels (Pesnell and Brown 1977). David (1994a) documented a general decline in wading bird nesting populations at Lake Okeechobee following the adoption of a higher lake-stage regulation schedule in 1978. In particular, the King's Bar colony site, which had previously been the largest perennial colony on the lake, was abandoned and has not been used since. However, Loftus et al. (1990) and Loftus and Eklund (1994) provide evidence that long-hydroperiod marshes generally support denser populations of forage fishes and macroinvertebrates. Similarly, Bildstein et al. (1990) found that White Ibises nesting in coastal colonies in South Carolina depended on high winter rainfall to encourage high crayfish (Procambarus sp.) productivity in nearby freshwater marshes. The adults often fed in salt marsh areas, but were forced to rely on the freshwater marshes to provide food for their nestlings, because the young birds cannot tolerate the high salt content of marine prey. Several studies have also indicated that wading birds often capitalize on surface-water recessions that concentrate prey (Kushlan et al. 1975; Kushlan 1976b; Browder 1976; Kushlan and Hunt 1979; Frederick and Spalding 1994), and nesting adults may depend on receding water levels during the breeding season to concentrate prey sufficiently to satisfy the needs of their growing young (Kahl 1964; Kushlan et al. 1975; Clark 1978). However, Ogden (1994) notes that Wood Storks may have only recently developed a strict dependence on the concentrating effects of surface-water recessions. He suggests that hydrologic manipulations have significantly reduced the prevalence of long-hydroperiod marshes, which has in turn led to a substantial reduction in the overall productivity of the Everglades. The reduction in productivity has meant that the storks must rely on the prey concentrating effects of recessions to succeed at all, whereas prior to widespread drainage such events may simply have helped to increase productivity to high levels. Such sensitivities render

wading birds ideal subjects for studying the effects of changing water levels at Lake Okeechobee.

Hydroperiod and water depths are, however, not the only potentially manageable factors that influence the ability of wading birds to exploit prey populations and reproduce successfully. Vegetation structure, for example, is likely of critical importance in determining both the diversity and abundance of prey (e.g., see Chick and McIvor 1994) and whether a bird can successfully access available prey. Sufficient vegetative cover must be present to provide safe habitat for small fish and invertebrates, but the birds must be able to both move about readily and visually detect approaching predators. Thick stands of tall grass or species such as cattail and sawgrass (Cladium jamaicense) probably physically impede access by most wading birds (see Hoffman et al. 1994). Cattail has dramatically expanded in abundance in areas subject to artificial eutrophication and is now considered a nuisance in many areas (Davis 1989; Richardson and Harris 1994; Richardson et al. 1994). In contrast, small forage fishes are generally scarce in very open habitats (Werner et al. 1977), and those that are present are likely difficult to capture. Thus, habitats featuring appropriate water depths and vegetation of moderate stature and structural diversity should provide the best foraging opportunities. Nutrient-rich canals, impoundments and bays often support extremely dense mats of water hyacinth and water lettuce (Pistia stratiotes) or very dense stands of Hydrilla intertwined with filamentous algae, to the point that fish and thus foraging wading birds might be excluded. However, moderate to high densities of Hydrilla unencumbered with thick filamentous algae often harbor high concentrations of small fishes (McIvor and Smith 1992; Chick and McIvor 1994), and thick surface mats of Hydrilla and floating mats of water hyacinth may provide the means for wading birds to access habitats too deep for wading (Chapter 2; and see

Murdich 1978). Inundation levels, nutrient inputs, and natural events such as freezes and fires all influence the distribution and composition of vegetation communities at the lake (Richardson et al. 1994), and therefore also influence the productivity of wading birds.

Lake Okeechobee is almost entirely surrounded by an earthen dike, and most water flows into and out of the lake are regulated by locks, hurricane gates, and pumping stations. Thus, the lake is now largely isolated from adjacent wetlands. Moreover, as mentioned previously, most of what used to be an extensive sawgrass marsh south of the lake is now the EAA, which is covered with sugar cane and rice fields and citrus orchards. In contrast, much of the area north and west of the lake has been converted to dairy farms and cattle pastures. Consequently, there is a stark contrast between the habitats available inside and outside the diked confines of the lake. Wading birds that nest on the lake can easily access both on- and off-lake habitats, and therefore management plans developed for the lake should recognize the potential influence of these alternative habitats. One issue of potentially great import concerns the possibility that highly disturbed and nutrient-enriched habitats such as agricultural ditches and cattle ponds may support elevated populations of the oligochaetes that serve as the first intermediate host for the nematode parasite Eustrongylides ignotus (Spalding et al. 1993; Frederick and Spalding 1994). This parasite has caused epizootic mortality among wading bird nestlings in the Everglades and elsewhere (Wiese 1977; Roffe 1988; Spalding et al. 1993), and reduced the survival and growth rates of Great Egret nestlings at Lake Okeechobee during my study (Spalding et al. 1994).

Wading Bird Project Objectives

With the above issues and concerns in mind, the primary goals of my research were as follows:

1) Begin to elucidate how habitat structure, hydrology, climate, and variation in the distribution and abundance of prey influence the temporal and spatial distribution, and nesting and foraging ecology of wading birds at the lake.
2) Assist in the development of conceptual models of the Lake Okeechobee ecosystem, specifically focusing on the interactions of biotic components and hydrology.

To achieve these goals, the major procedural objectives of my research were as follows:

1) Document through regular aerial surveys the foraging distribution and abundance of all common species of wading birds throughout the littoral zone of the lake and in select perennial wetlands adjacent to the lake.
2) Document through aerial surveys the location, composition, and history of all nesting colonies on and in close proximity to the lake.
3) Conduct intensive studies of marked nests in select, geographically dispersed colonies on the lake to document the reproductive success and productivity of all common species.
4) Monitor nestling diet through opportunistic collection of regurgitant samples during colony checks.
5) Document nestling growth rates for focal species by gathering measurements from representative samples of nests in each colony with marked nests.

6) Document through aerial following flights the foraging habits of nesting adults during the brood-rearing phase.

7) Observe foraging adults primarily in habitats corresponding to those chosen by nesting adults--identified through following flights (Objective 6)--to quantify foraging success and prey choice.

8) Follow observations of foraging birds (Objective 7) with prey sampling to quantify prey abundance and confirm prey species representation.

9) Integrate the above data with hydrologic and climatic datasets and annual vegetation maps to identify the environmental conditions that lead to successful foraging and high reproductive productivity among wading birds at the lake.

10) Program a population energetics model to conceptually integrate the various aspects of wading bird ecology at the lake and to simulate the responses of wading birds to fluctuating environmental conditions.

The primary working hypotheses on which I based my research program included the following:

Distribution and Abundance, and Foraging Ecology:

1) Patterns of abundance and distribution are primarily a function of hydrology.

a) The stage level sets the ultimate spatial boundaries to foraging.

b) The magnitude and duration of drying trends determine whether prey are concentrated or dispersed.

c) Hydroperiod and levels of inundation influence the vegetative structure of habitats.

2) Foraging birds prefer mixes of emergent vegetation of moderate density and height that provides refuge for prey species, but does not unduly hinder a bird's

progress through the habitat nor restrict its ability to remain vigilante against predators and other disturbances.

3) Lakewide population trends will in part reflect environmental conditions occurring elsewhere in Florida and the southeast. In particular, because it is a large lacustrine system, Lake Okeechobee may constitute a significant regional refuge during periods of drought.

4) The availability of profitable foraging habitat nearby but outside the diked boundaries of the lake often will provide a level of independence from on-lake hydrology.

Nesting Ecology:

1) The timing of nesting activities is a complex function of environmental cues--including aspects of hydrology (water level, drying rates, rainfall patterns), climate (temperature, storm frequency and severity), and prey population dynamics--acting in conjunction with elements of social facilitation.

2) The location of nesting colonies is constrained primarily by the availability of suitable nesting substrate--e.g., willow heads. The distribution of willow is a function of hydroperiod, and wading birds chose colony sites surrounded by water that is deep enough to discourage invasion by mammalian predators. Therefore, the location of nesting colonies is a function of hydrology, specifically lake stage and hydroperiod.

3) Colony locations are secondarily constrained in proximity to favorable foraging grounds; again primarily a function of hydrology and the distribution of appropriate vegetative cover.

4) The abandonment of entire colonies is primarily a function of stochastic events such as temperature fluctuations, large-scale wind and rainfall events, and

unexpected shifts in the hydrologic regime that lead to deterioration of foraging conditions. Excessive predation or disturbance, and disease or parasite epidemics may also induce abandonment.

5) Mean lakewide whole-nest survival and productivity rates vary between years primarily as a function of hydrology--lake stage, hydroperiod, and drying rates--through its influence on the abundance, distribution, and accessibility of prey resources. However, as with colony turnover rates, other factors such as predation, disturbance, and disease or parasite outbreaks may significantly impact overall nest survival rates in certain years.

6) Colony-specific rates of nest success and productivity more closely reflect local hydrologic conditions and the health of adjacent habitats and prey populations, as well as unique aspects of the colony site structure and local predation, disease, and parasite phenomena.

7) Variation in the overall productivity of nesting events is manifest primarily as changes in the mean survival rate of whole nests, rather than as changes in the mean productivity of successful nests.

8) Nest failures and abandonments during the incubation phase are more often a function of excessive disturbance or inclement weather, whereas failures during the nestling phase are more regularly a function of the abundance and accessibility of prey resources and secondarily of the prevalence of parasite and disease outbreaks. Predation events may affect failures during both stages.

Dissertation Format and Content

Beyond this introductory chapter, this dissertation is divided into five main chapters and a final summary chapter. I composed each of the five main chapters as stand-alone manuscripts. Therefore, there is some redundancy in the introductory sections and reference figures. In Chapter 2, I summarize my findings concerning the distribution and abundance of foraging birds with relation to hydrologic influences, and discuss an analysis of foraging habitat selection relative to vegetation community types. In Chapter 3, I summarize my findings concerning the foraging habits of nesting adults, which I documented through aerial following flights. In Chapter 4, I summarize my findings concerning the history of nesting and causes of failure during the study, and discuss general trends in reproductive effort, success, and productivity. In Chapter 5, I discuss a comprehensive logistic regression analysis I conducted to further elucidate relationships between nest failure rates and a suite of nest-situation, hydrology, and climate variables. I then complete the primary presentation with Chapter 6, wherein I discuss my effort to program a population model for Great Egrets. I do not herein discuss in detail the results of my efforts to study nestling growth and diet or the foraging success of birds in different habitats (and the associated prey sampling). I will cover these topics in future manuscripts.

CHAPTER 2
FORAGING HABITAT SELECTION IN RELATION TO HYDROLOGY AND VEGETATIVE COVER

Introduction

Wading birds are highly visible, top-level consumers and are considered bioindicators of change in hydrological and ecological conditions in wetland ecosystems (e.g., Custer and Osborn 1977; Curry-Lindahl 1978; Hafner and Britton 1983; Bildstein et al. 1990; Kushlan 1986b, 1993; Ogden 1994). Nesting populations of most species have declined dramatically over the past few decades (Ogden 1978a, 1994; Kushlan et al. 1984) most likely due to habitat degradation and ill-advised hydrological manipulations (Kushlan 1986a; Walters et al. 1992; Bancroft et al. 1994; Frederick and Spalding 1994; Ogden 1994). In an effort to elucidate the causes of decline, researchers have paid considerable attention to documenting population trends and the nesting and foraging ecology of wading birds in Florida Bay and the Everglades region (Kushlan et al. 1975; Browder 1976; Bancroft and Jewell 1987; Frederick and Collopy 1988, 1989a, b; Bancroft et al. 1990; Hoffman et al. 1994; Frederick et al. 1992; Frederick and Loftus 1993; Frederick and Spalding 1994). In contrast, Lake Okeechobee--historically the primary source of water, along with rainfall, for the Everglades--has been little studied (but see Zaffke 1984; David 1994a, b) yet is the third largest freshwater lake within the United States (1,732 km^2 surface area; Herdendorf 1982) and supports several large mixed-species wading bird nesting colonies each year (Chapter 4; David 1994a).

Studies at Lake Okeechobee are likely to reveal unique aspects of wading bird ecology and unique patterns of response to fluctuating environmental conditions for several reasons. The lake ecosystem features a large expanse of emergent marsh (typically about 400 km^2) similar to the wet prairie marshes of the Everglades and other palustrine systems in southern Florida (Fig. 2-1). However, the lake ecosystem differs from Everglades-type wetlands in that it also features a large, relatively deep and persistent open-water pool. This difference means that populations of mobile aquatic organisms--such as the forage fishes, amphibians, and macroinvertebrates that wading birds feed on--probably can survive during periods of even extreme drought by seeking refuge along the edges of the central pool. Recolonization and recovery rates should therefore be more rapid, and for this reason, overall aquatic productivity may be higher than in strictly palustrine systems (cf. Loftus and Eklund 1994). Moreover, because large lacustrine systems like Lake Okeechobee include a deep-pool region where prey can seek refuge, such systems may also serve as critical regional drought refuges for vagile species such as wading birds. The lake ecosystem also includes extensive beds of submerged vegetation (Zimba et al. 1994) not found in shallow palustrine systems, and sampling revealed very high concentrations of forage fish and grass shrimp (Palaemonetes paludosus) in some of these habitats (McIvor and Smith 1992; Chick and McIvor 1994). Furthermore, because the lake is almost entirely surrounded by a large earthen dike, there is an abrupt transition from extensive marsh and open-water habitats inside the dike to a wide variety of natural and artificial wetland habitats outside the dike. The latter include: the Kissimmee River and Fisheating Creek floodplains (see Fig. 2-1); diverse pocket and slough wetlands interspersed with cattle pastures to the north and west; myriad agricultural field ditches and canals to the south and east; and residential canals and retention ponds in several areas. The lake region

Figure 2-1. A geographic overview of the Lake Okeechobee area.

thus provides wading birds with an unusually diverse array of foraging opportunities within a relatively limited area.

The multidisciplinary Lake Okeechobee Ecosystem Study was initiated in 1988 to provide baseline ecological data to the South Florida Water Management District (SFWMD) and facilitate the development of an ecologically sound management strategy for the lake. The primary goal of the project was to increase our understanding of how hydrologic fluctuations and cultural eutrophication influence water quality and the ecological dynamics of the vegetation and wildlife communities of the lake. Aumen (1994) discusses the management history of the lake and the impetus for the study in more detail. My primary responsibility was to determine how lake-stage regulation schedules and other management practices employed by the U. S. Army Corps of Engineers and the SFWMD influence the population dynamics of wading birds at the lake. In this chapter, I present the results of using aerial surveys to document the distribution and abundance of nine species of foraging wading birds on the lake from August 1988 through August 1992. Specifically, I sought to elucidate how the distribution and abundance of foraging wading birds changed in relation to fluctuating water levels, and to determine whether the birds' use of foraging habitat reflected preferences for certain vegetation assemblages.

The study period spanned both high water years and a two-year drought that resulted in a 10-year low lake stage in May 1990. A series of fires and freezes further contributed to pronounced interannual shifts in the composition and distribution of vegetation assemblages (Richardson and Harris 1994). To elucidate relationships between wading bird habitat selection and changes in hydrology and vegetation, I integrated my wading bird foraging-dispersion data with annual vegetation maps (Richardson and Harris 1994) and hydrologic data derived from stage recorders and a

hydrologic model (Richardson and Hamouda 1994). I thereby gained knowledge about species-specific habitat choices and their ecological significance. I gained insight about the relative importance to wading birds of several species of exotic and nuisance vegetation that concern resource managers in Florida. I was also able to elucidate the combinations of hydrology and vegetative structure that attracted the largest numbers and variety of wading birds to the lake. Along with these studies of foraging dispersion, I also documented the foraging efficiency and prey selection of individual birds in different habitats, and studied the nesting ecology of common species through aerial surveys and ground-based monitoring of marked nests (Chapters 3-5; Collopy and Smith 1991; McIvor and Smith 1992). The integration of such information provided the basis for projecting management strategies that should increase the occurrence of favorable foraging conditions on the lake and enhance the productivity of wading bird nesting efforts.

Methods

Study Area and Subjects

A geographic overview of the Lake Okeechobee area is provided in Figure 2-1, with primary wading bird nesting colonies, hydrologic gauging stations, and key regions, waterways, towns and other landmarks identified. I will frequently refer to areas and landmarks depicted on this map without reference to the figure. Aumen (1994) provides an overview of the physiography and hydrology of the lake. Richardson and Hamouda (1994), Richardson and Harris (1994), and Richardson et al. (1994) discuss in detail the hydrology and vegetation community dynamics of the lake.

I tallied the following species separately on all surveys: Great Blue Heron (and the unique Great White Heron subspecies), Great Egret, Snowy Egret, Tricolored Heron, Little Blue Heron, White Ibis, Glossy Ibis, Wood Stork, and Roseate Spoonbill. Cattle Egrets only rarely foraged on the lake and I did not keep track of their numbers. It is difficult to distinguish immature Little Blue Herons and Snowy Egrets from the air. Ground-based observations of mixed-species feeding flocks indicated that immature Little Blue Herons always constituted less than 5% of the total number of small white herons and egrets in such flocks (unpubl. data). During this study, I never saw more than three or four immature Little Blue Herons together in one group, and these were usually with other adult Little Blue Herons. Therefore, I lumped all Snowy Egrets and unidentified small white ardeids into the category Small White Ardeids (SWA) and conducted analyses only on the combined group. However, for convenience, and because I am confident of the comparative rarity of immature Little Blue Herons, I will refer to results for the SWA group as if they were for Snowy Egrets alone. I categorized all positively identified immature Little Blue Herons as such, not as SWA. Tricolored Herons and adult Little Blue Herons are also difficult to distinguish from the air when in mixed flocks, and many were assigned to the category Small Dark Ardeids (SDA). In this case, I conducted separate analyses on data for identified individuals and for the combined group, and compared results before developing interpretations. Great White Herons, Wood Storks, and Roseate Spoonbills were not common enough on the lake to be included in statistical analyses of habitat selection.

On all foraging-dispersion surveys, birds were classified as either foraging, commuting (i.e., obviously in transit, as opposed to birds that flushed as the plane approached) or roosting (i.e., birds perched in shrubs or trees). I included only foraging birds in analyses of habitat selection, but included all individuals in population

estimates. I tallied birds attending nests during separate weekly surveys and do not consider these data here (see Chapter 4).

Survey Design

I employed a three-part aerial survey design to document the distribution and abundance of foraging wading birds on and adjacent to the lake (Fig. 2-2). The survey program included: 1) a series of belt transects to sample most of the extensive west-side littoral region; 2) a standardized but nonsystematic survey route to cover the eastern margin and the southern islands; and 3) five complete-count block surveys to cover the Eagle Bay Island and adjacent marsh area at the north end of the lake, and four other perennial wetlands adjacent to the west side of the lake. I conducted the full set of surveys over a two-day period, usually transects on the first day and other surveys on the second. I completed monthly survey sets from August 1988 through early January 1989. This was the only fall season I sampled, and an initial variation in the survey design (different lay-out and attendant visibility biases; see McIvor and Smith 1992) rendered the data less compatible with those from subsequent surveys. Therefore, I did not include the early data in analyses of habitat selection, but did include the data in plots showing trends in lakewide abundance. I adopted the new "standard" transect survey design in late January 1989, and subsequently completed survey sets twice per month January through August 1989-1991 (except that I was unable to begin surveys until March in 1991 due to unforeseen difficulties associated with renewal of a low-altitude flight permit) and monthly January through August 1992. The January through August period corresponded to the usual wading bird nesting season (see Chapter 4). The reduction to monthly surveys in 1992 was a contract-related compromise that involved budget and time constraints.

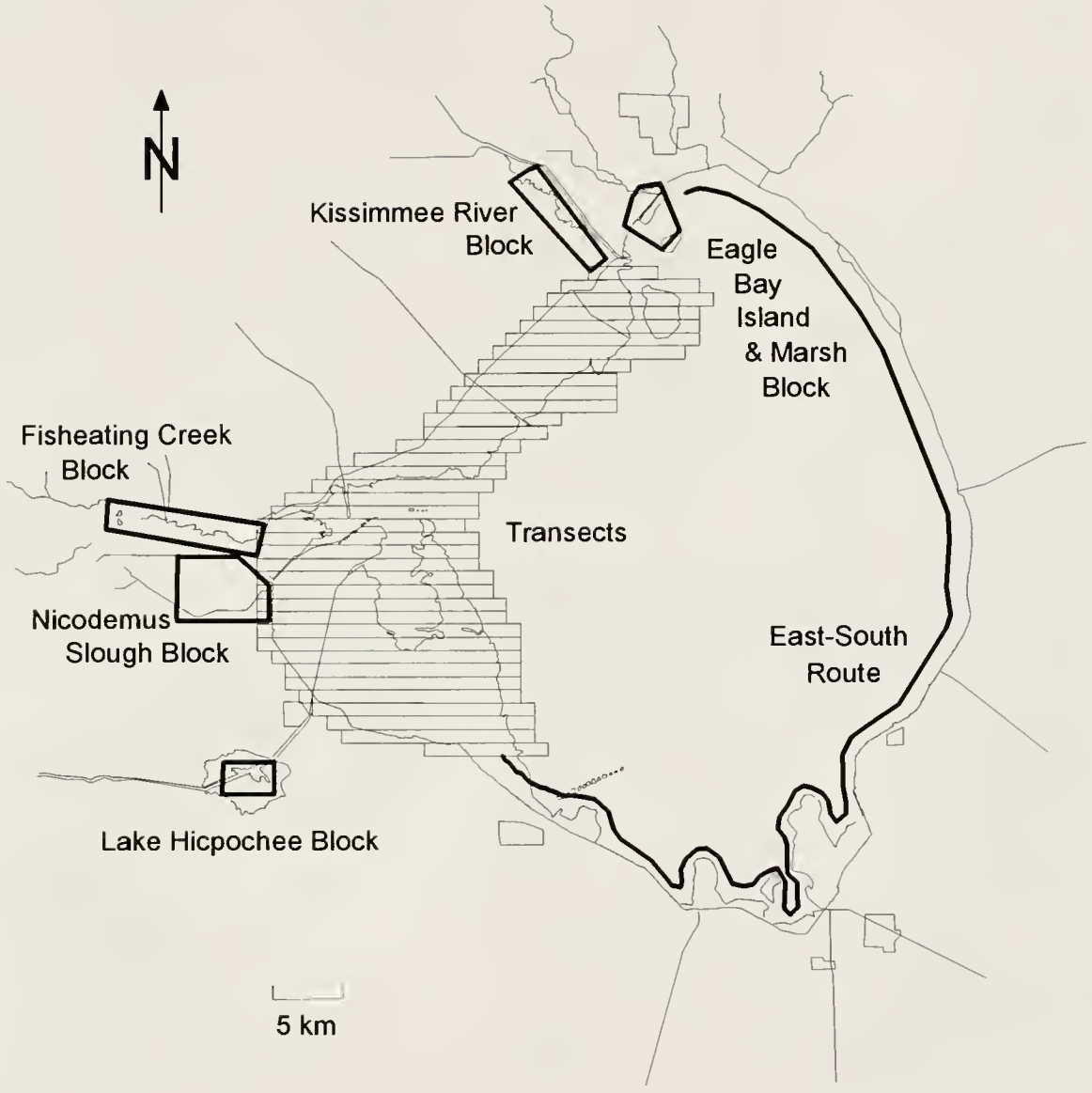


Figure 2-2. Aerial survey program used to document the distribution and abundance of foraging birds.

The standard transect surveys included 37 kilometer-wide, east-west transects that covered most of the western littoral zone (Fig. 2-2). Each survey round began at the north end with transect #1, continued southward with odd numbered transects and alternating start points (i.e., east or west end), and then reversed northward to cover the remaining even numbered transects. This protocol helped ensure (pers. observ.) that flushed birds had time to return to their original foraging spots before an adjacent transect was surveyed, and thereby reduced the chance of double counting. Transect surveys were flown between 0700 and 1400 hrs EST in a Cessna 172 fixed-wing aircraft at an air speed of 80-90 knots (148-167 km h^{-1}) and an altitude of 76 m above ground level. An aviation-grade LORAN C unit enabled navigation along latitude lines running down the center of each transect belt. Myself and a second observer (a different field assistant each year 1989-1991; otherwise a mix of four other trained observers) sat on opposite sides of the plane and counted all birds observed within 150 m wide strips extending outward from the side of the plane. The count zones were delineated as described in Norton-Griffiths (1975), and the setup rendered a 30% sample of each transect belt. I derived final population estimates using Jolly-Seber II techniques (Norton-Griffiths 1975). Longitude coordinates recorded with each bird or group of birds observed provided the means for assigning all observations to 1-km x 1-km grid cells. This enabled the production of GIS distribution maps and analyses of habitat selection.

The East-South Route survey followed a standardized but unsystematic path along the eastern and southern margins of the lake. The survey path included regular diversions over the interior of wet islands and other areas where wading birds congregated, such that all useable habitat was surveyed and all visible birds were counted. I was the sole observer, and the flight speed and altitude conformed to

transect survey protocol. I allocated observations to only coarse-scale geographic regions that were incompatible with the 1 km^2 scale of the transect grid. I therefore did not include these data in statistical analyses of habitat selection.

The block-surveys covered portions of five structurally varied wetland areas outside the diked boundaries of the lake, but I chose not consider these data in this dissertation (I intend to produce a separate manuscript summarizing the data). The northern-most block survey also covered the Eagle Bay Island area within the boundaries of the lake, which was an important foraging and nesting area. I was the sole observer on all block surveys, the flight speed and altitude conformed to transect survey protocol, and I searched each block area until I had counted all visible birds. I mapped the locations of all birds on overlays of satellite imagery, later assigned each bird to 1-km x 1-km grid cells, and then integrated the data with the transect-survey GIS databases.

I generated lakewide population estimates by adding counts from the Eagle Bay Island and East-South Route surveys to extrapolated estimates derived from the transect surveys.

Hydrology, Vegetation, and Analyses of Habitat Selection

I sought to derive functions that effectively summarized relationships between lakewide bird abundance and hydrologic trends. Responses to variation in the mean lake stage were of particular interest, because this is often the parameter of concern among managers. Stage data for the lake are geographically limited, particularly for the emergent marsh zones. I obtained two sets of daily stage measurements from the SFWMD that spanned the entire study period. The first series was collected at a gauging station located in the central, open-water portion of the lake (Fig. 2-1). The

second series was collected at a station located in the interior of the emergent marsh zone east of Moore Haven (Fig. 2-1). The two stage records matched closely at stages above about 4.3 m NGVD, but diverged at lower stages (Fig. 2-3; NGVD = National Geodetic Vertical Datum of 1929, essentially equivalent to height above mean sea level; for convenience, I will henceforth omit the NGVD qualifier). The discrepancy arises because the emergent marsh zones along the western margin become hydrologically isolated from the open water portions of the lake at low stages (Richardson and Hamouda 1994). At lower stages, local rainfall patterns determine water levels in the upper-elevation marshes, and short-term fluctuations are pronounced. Conversely, the open-water stage is a function of watershed-scale rainfall patterns and to a lesser degree artificial manipulations implemented to meet mandated regulation schedules. Short-term fluctuations are not pronounced because the data reflect larger-scale hydrologic trends. I chose to use the open-water dataset for three reasons. First, despite considerable differences in the magnitude of fluctuations and response times, the general patterns of fluctuation shown in the two datasets were similar; i.e. periods of rising or receding water generally matched (Fig. 2-3). Second, the distribution of rainfall over the marsh zones was highly uneven from day to day (pers. observ.). For this reason, I felt that the open-water data provided a better index to basin-average conditions. Lastly and most importantly, there were large gaps (36-57 days) in the marsh dataset during the wading bird nesting season in 1989, 1991 and 1992, while the largest gap in the open-water dataset was only two days.

From the stage data, I derived additional variables to represent the mean rate of change in surface-water levels (cm day^{-1}) over various antecedent time intervals. I calculated the differences between the stage at survey time and that recorded 30, 60, 90 and 120 days earlier, and then divided each difference by the appropriate number of

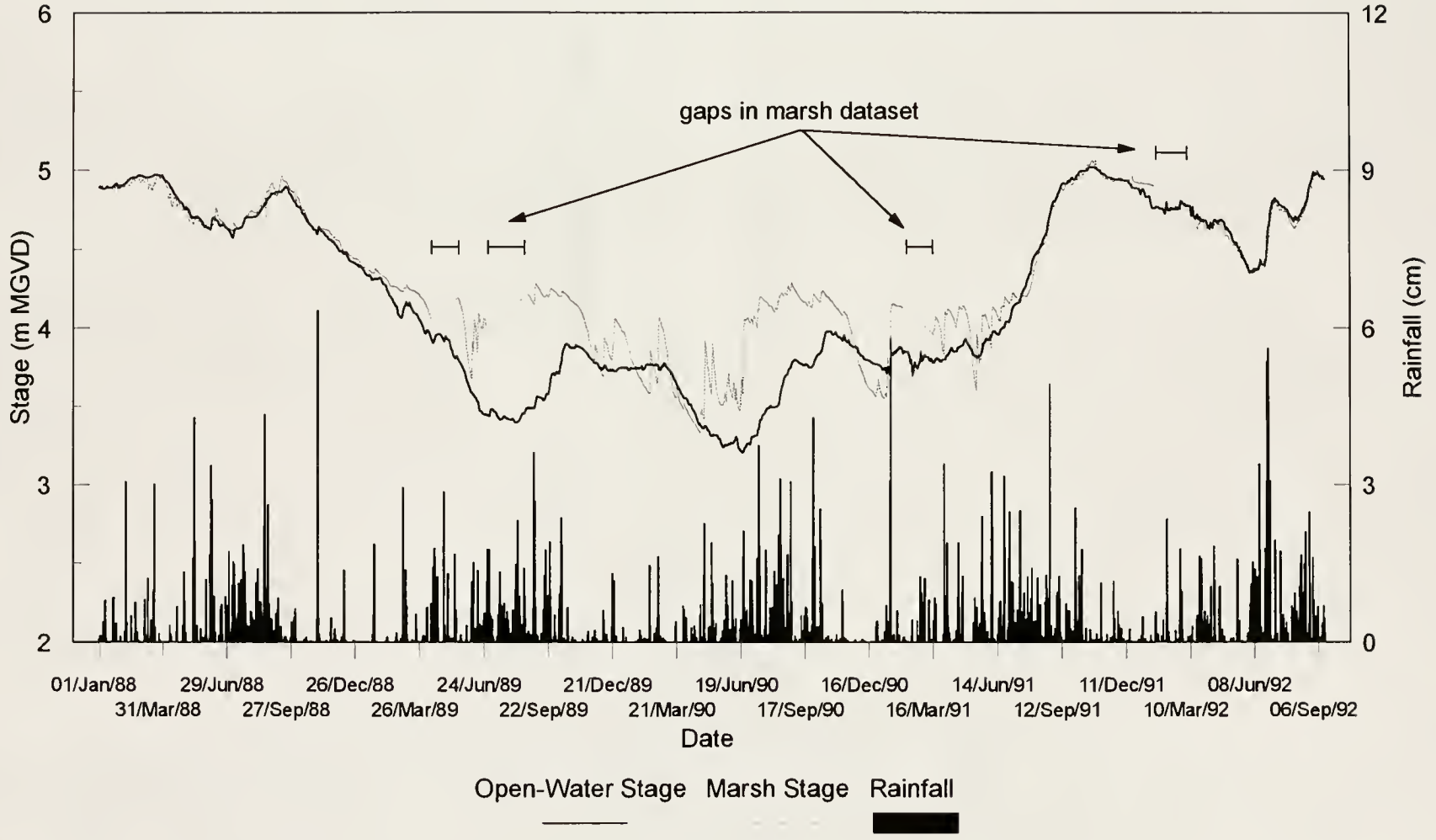


Figure 2-3. Comparison of open-water and Moore Haven marsh daily lake stage records, shown in relation to estimates of average daily rainfall for the Lake Okeechobee basin: January 1988 - September 1992.

days. For convenience, I will refer to the latter as "drying-rate" variables, but note that a negative value indicates a surface-water recession or drying trend, whereas a positive value indicates rising water. I then regressed bird counts against each individual hydrologic parameter, and analyzed multiple regression models of bird counts versus pairs of stage and drying-rate variables in an effort to derive the best predictive model.

I also visually compared the distributional patterns of foraging wading birds against bimonthly GIS maps of water depth derived from the OKEEHYDRO model discussed in Richardson and Hamouda (1994). The OKEEHYDRO model was programmed to output mean water levels for the 15th and last day of each month, for a series of 915-m x 915-m grid cells covering all but the central, open-water section of the lake. Each output file was then resampled (using READOKEE; Richardson 1993) to produce ERDAS (1991) GIS maps of water depth with a spatial resolution of 100-m x 100-m. I then used another custom program (POLYSTATS, Richardson 1993) to calculate bimonthly mean water depths for each of the 507 1-km x 1-km grid cells that covered my transect (489 cells) and Eagle Bay Island (18 cells) survey areas.

Richardson and Harris (1994) generated annual vegetative cover maps by classifying SPOT satellite images using ERDAS GIS software. Each map represented a blend of data from one spring and one fall scene. The pixel resolution was 9.15-m x 9.15-m. A total of 30 classes of vegetation (including a class for non-vegetated open water) were represented; 27 of these occurred in the transect and Eagle Bay Island survey areas. Because the spatial resolutions of the vegetation and bird-distribution maps did not match, it was necessary to rescale the vegetation maps to match the bird maps. I accomplished this in two steps. First, I overlayed my survey grid matrix on each vegetation map and calculated a vector of class-specific relative cover statistics for each grid cell using POLYSTATS (Richardson 1993). Second, I derived a new

vegetation classification scheme by using the nearest-centroid clustering procedure in SAS (FASTCLUS--a clustering algorithm specifically designed for aggregating large numbers of observations; SAS Institute Inc. 1988) to divide the 4 x 507 sets of cell-specific cover statistics into a reduced number of new aggregate vegetation classes. The new classification scheme then became the basis for calculating expected bird densities in chi-square (χ^2) tests of independence (Sokal and Rohlf 1981: 708) designed to determine whether foraging birds actively selected or avoided certain vegetation assemblages. I discuss the details of these tests in the results section as I present summary charts.

Results and Initial Discussion

Abundance of Foraging Birds and Hydrologic Trends

Total combined-species population estimates for the study are shown in relation to mean daily lake stage in Figure 2-4. Species-specific plots are shown in Figures 2-5 - 2-7. Appendix A contains a list of the actual counts by survey and species. I did not include birds attending nests in these totals, but the addition of these relatively small numbers (see Chapter 4) did not appreciably alter the trends shown.

The foraging-population counts of most species followed similar trends during the study. Counts of all species except Glossy Ibises increased dramatically in response to the protracted surface-water recessions and low lake stages of the 1989 and 1990 drought periods. Counts were generally lower at higher lake stages--especially above 4.4-4.5 m--in late 1988 and early 1989, and in 1992 (also see Zaffke 1984 and David 1994b). Data for the uncommon, non-nesting Wood Storks and Roseate Spoonbills further confirmed that the drought-induced low and declining lake

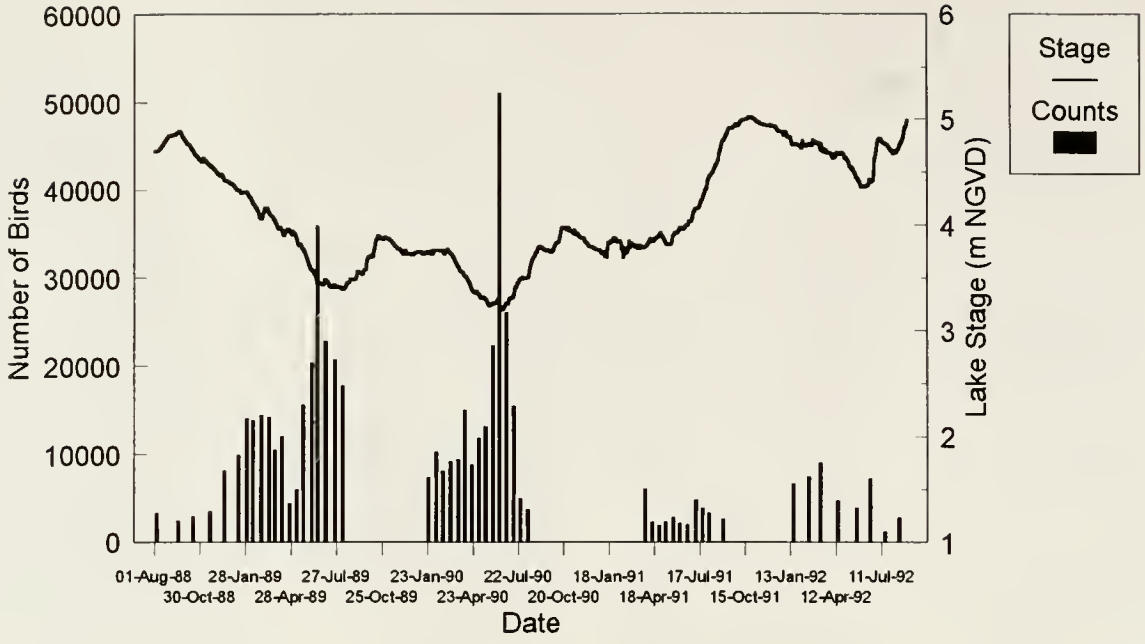


Figure 2-4. Combined-species wading bird population estimates, excluding birds at nests, in relation to daily lake stage: August 1988 - August 1992. Gaps in bird counts indicate no surveys.

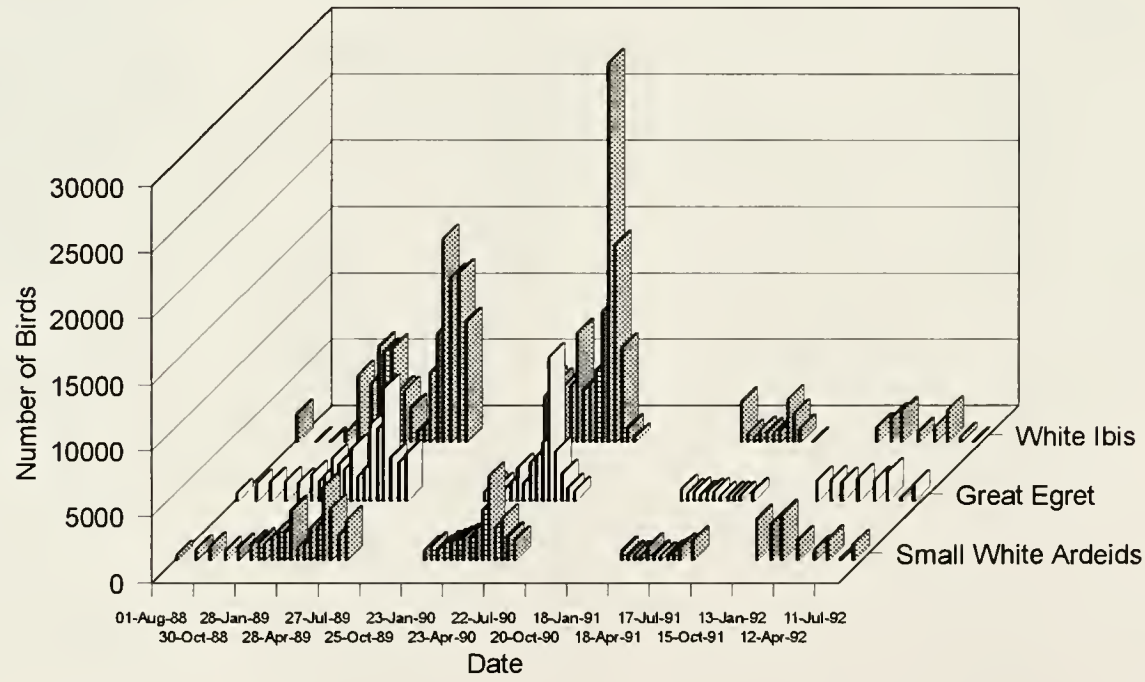


Figure 2-5. Population estimates for White Ibises, Great Egrets, and Small White Ardeids (i.e., Snowy Egrets and some immature Little Blue Herons), excluding birds at nests: August 1988 - August 1992. Gaps in records indicate no surveys.

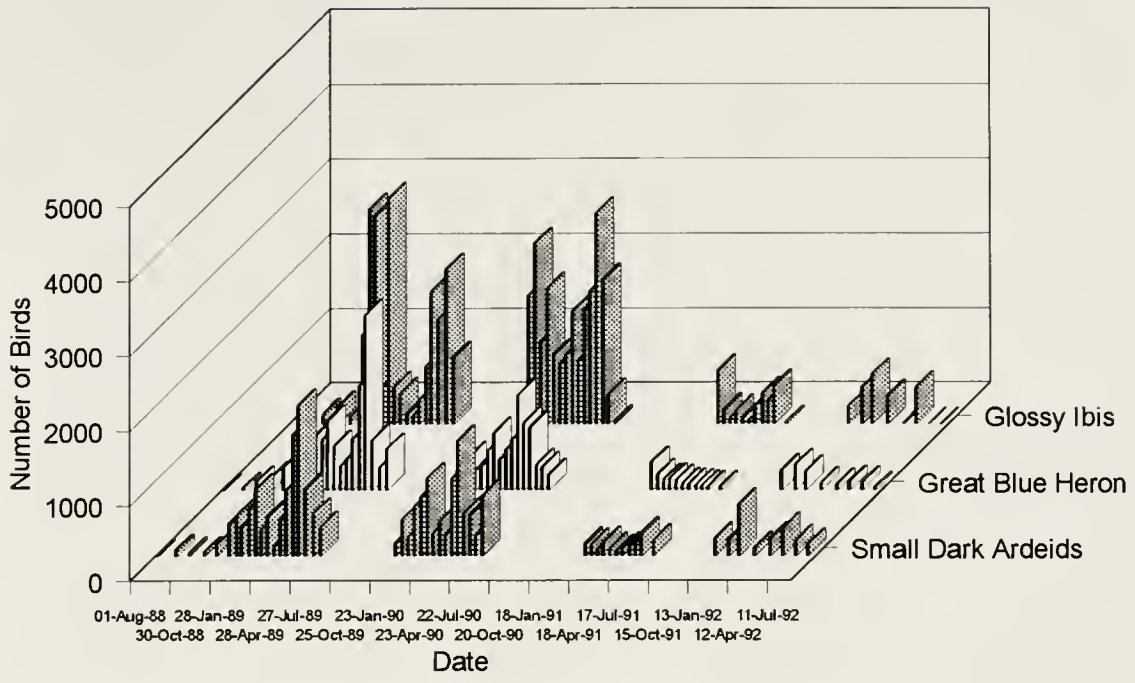


Figure 2-6. Population estimates for Glossy Ibises, Great Blue Herons, and Small Dark Ardeids (i.e., Tricolored and adult Little Blue Herons), excluding birds at nests: August 1988 - August 1992.

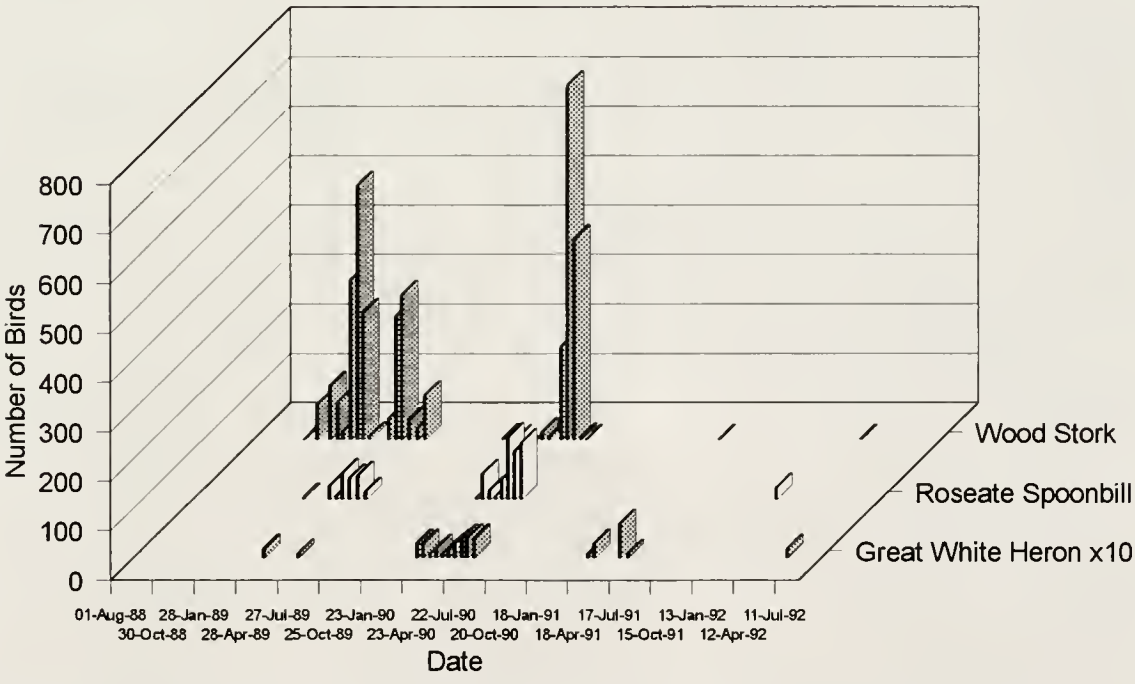


Figure 2-7. Population estimates for Wood Storks, Roseate Spoonbills, and Great White Herons: August 1988 - August 1992.

stages attracted an unusual number and variety of birds to the lake (Fig. 2-7). The drought concentrated prey in shallow pools, canals, alligator holes, and airboat trails (cf. Kushlan et al. 1975; Kushlan 1976b; Kushlan and Hunt 1979), and especially in beds of submerged vegetation at the outer edges of the littoral zone (Chick and McIvor 1994). These rich prey resources were undoubtedly an important attractor, but the unusually high numbers and diversity of birds also suggested that the lake served as an important regional drought refuge for wading birds. The lack of a protracted spring recession in 1991 apparently produced less-favorable foraging conditions, despite moderate lake stages between 3.7-4.3 m. Populations initially were higher in 1992, probably because the year began with a moderate recession. However, consistently high lake stages restricted access despite favorable drying trends, and numbers declined rapidly later in the season when the recession reversed.

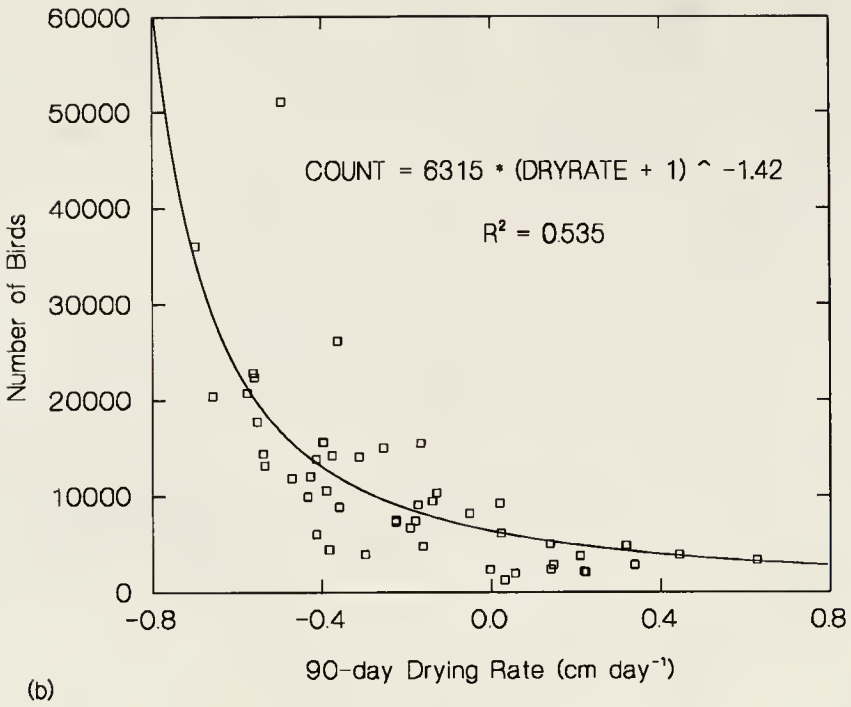
As mentioned previously, I was unable to begin standard transect surveys until late-March in 1991. However, during this time I conducted higher-altitude surveys of the block and East-South Route regions, and perused the transect area to document large flocks. These informal surveys confirmed that numbers of most species remained low throughout the 1991 season. They also confirmed that White and Glossy ibises were more abundant early in the season, although the numbers were never appreciably higher than during the 30 March survey (Figs. 2-5, 2-6).

Glossy Ibises were unique in not showing the most dramatic increase in numbers at the lowest lake stages in 1989 and 1990 (Fig. 2-6). Instead, the species was more abundant earlier in 1989 and as abundant early in 1990 as it was during the peak low-water periods each season. This trend could indicate a greater preference for moderate lake stages, perhaps because a wider variety of foraging habitats is then available. However, the species showed a consistent bimodal trend in numbers each

year, with lower numbers during the middle of the season. The consistency of the pattern contrasted markedly with the inconsistency of the concurrent hydrologic conditions. As mentioned, the displayed population totals do not include birds that were attending nests, and therefore the mid-season population estimates for common nesting species slightly underrepresent the actual population size. However, Glossy Ibises nested on the lake irregularly and only in small numbers during the study (pers. observ.). Therefore, the bimodal pattern was more likely evidence that the species usually emigrated to other nesting grounds. The same bimodal trend in numbers was evident to a lesser degree for White Ibises, and was least pronounced in 1990 (Fig. 2-5) when White Ibises initiated the most nests at the lake (Chapter 4).

Counts of all common species declined during March and April 1989 (Figs. 2-5, 2-6), and again none of the declines were accounted for by on-lake nest numbers. The temporary general decline in numbers corresponded to one primary (0.11 m over 12 days) and several lesser reversals in the drying trend that began at the end of February and continued through March (Fig. 2-4). The brief drop in Wood Stork numbers confirmed that a nesting exodus was not involved; Wood Storks did not nest at the lake during the study and returned when surface-water levels began to recede again (Figs. 2-4, 2-7). A freeze that occurred at the end of February--coincident with the onset of the primary reversal--probably added to the negative impact. Cold temperatures cause small fish to become less active and flee, burrow and hide more readily when disturbed, which probably renders it more difficult for wading birds to secure prey (Frederick and Loftus 1993). The combination of cold temperatures and reversals in the drying trend contributed to the abandonment of many Great Egret nests at this time (Chapters 4, 5).

Plots of combined-species bird counts versus mean lake stage and the drying-rate variables indicated distinctly non-linear trends (e.g., Fig. 2-8). All plots showed that



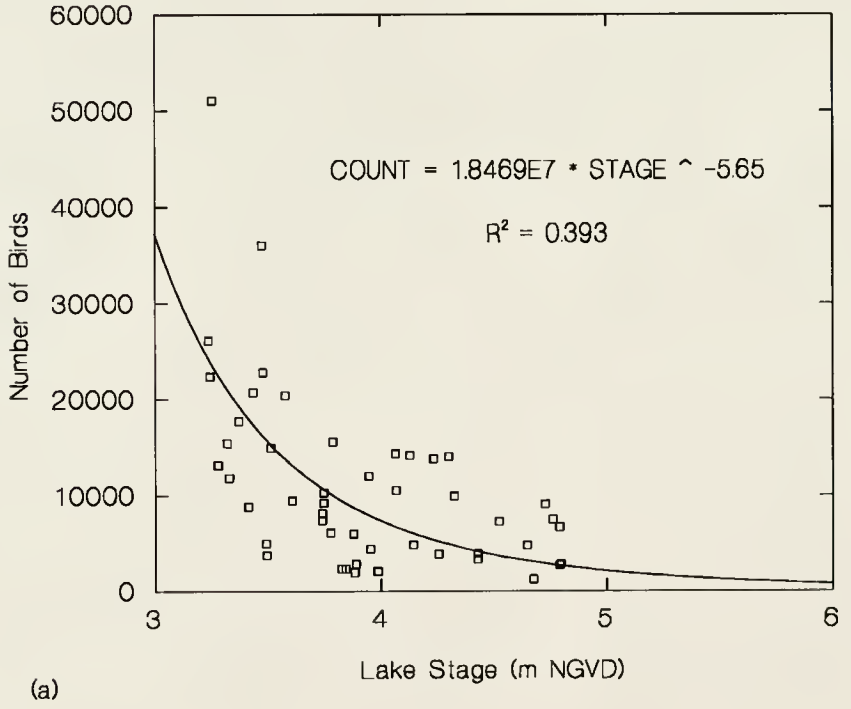


Figure 2-8. Non-linear regression of combined-species wading bird population estimates versus a) daily lake stage and b) 90-day antecedent surface-water drying rate (n = 49; curves fit using SYSTAT, Wilkinson 1990).

the foraging population grew at an increasing rate as the stage dropped and the drying rate increased. Power functions of the form Y = A * X ^ -B fit the data best, although negative-exponential functions of the form Y = A * EXP(-B * X) fit nearly as well. A power-function regression of counts versus lake stage yielded an adjusted R^2 of 0.393 (Fig. 2-8; n = 49, residual df = 47; model fit using SYSTAT, Wilkinson 1990). However, a similar regression of counts versus the 90-day drying-rate variable yielded the highest R^2 of 0.535 (Fig. 2-8). Multiple regression models including the additive effects of stage and different drying-rate variables yielded only marginal improvement. None of the models fit by the SYSTAT program adequately accounted for the unusually high peak in numbers at the height of the drought in 1990. This lent additional support for the contention that Lake Okeechobee served as an important regional drought refuge for wading birds. In other words, the initial response trend may have reflected the benefits of increasingly concentrated prey, but the accelerated response at the lowest stages probably reflected the drought-refuge effect eluded to above.

I based the choice of regression models on measures of statistical fit rather than a specific theoretical justification. Ultimately, bird abundance probably would reach an asymptote and eventually decline if surface-water levels continued to drop, especially if the decline outpaced the spread of submergent vegetation. Thus, a maxima function of the form Y = A * X * EXP(-B * X) may be the more appropriate theoretical model, but no data exist to test this hypothesis. Regardless, wading birds were attracted to the lake in ever larger numbers as the lake stage dropped, primarily because prey were increasingly concentrated in receding waterways and isolated pools. It is likely that the benefits of concentration accrue slowly at first, and then more rapidly when prey concentrations reach levels sufficient to accommodate certain behavioral shifts among the foraging birds. For instance, Kushlan (1976c, 1979) found that White Ibises usually

do not preferentially select fish as prey unless they are highly concentrated by receding water. There may be a general threshold of concentration above which wading bird foraging is greatly enhanced because the standard evasion tactics of small fishes and other prey cease being effective. If so, some form of non-linear wading bird population response would be expected.

Patterns of Distribution and Hydrologic Trends

Select pairs of water depth and combined-species bird distribution maps covering the transect and Eagle Bay Island survey areas are shown for the 1989-1992 seasons in Figures 2-9 - 2-12. I chose the series to highlight major shifts in distribution that occurred during the study, primarily as a result of changing hydrologic conditions. Most species followed similar distributional trends, with some variations discussed in the following sections. Only the largest Great Blue Herons and Great Egrets can wade in water near 50 cm deep; most species are constrained to depths below 20-30 cm depending on their leg length (e.g., see Kushlan 1986a). However, thick vegetation may provide support and allow access to deeper habitats. This often was the case in the Fisheating Bay area where thick floating mats of water hyacinth and thick surface mats of Hydrilla were prevalent. In addition, Great Egrets often took advantage of thick decumbent stands of Eleocharis and Panicum for support in the deeper wet prairie areas of Moonshine Bay. Thus, the maps include instances where birds were observed in cells with a mean water depth greater than 50 cm. Furthermore, the 1 km^2 spatial resolution of the water depth data, and the fact that I lumped the data into only five depth categories, obscured fine-scale topographic detail. Consequently, the maps also include instances where birds were observed in cells with a mean depth of zero.

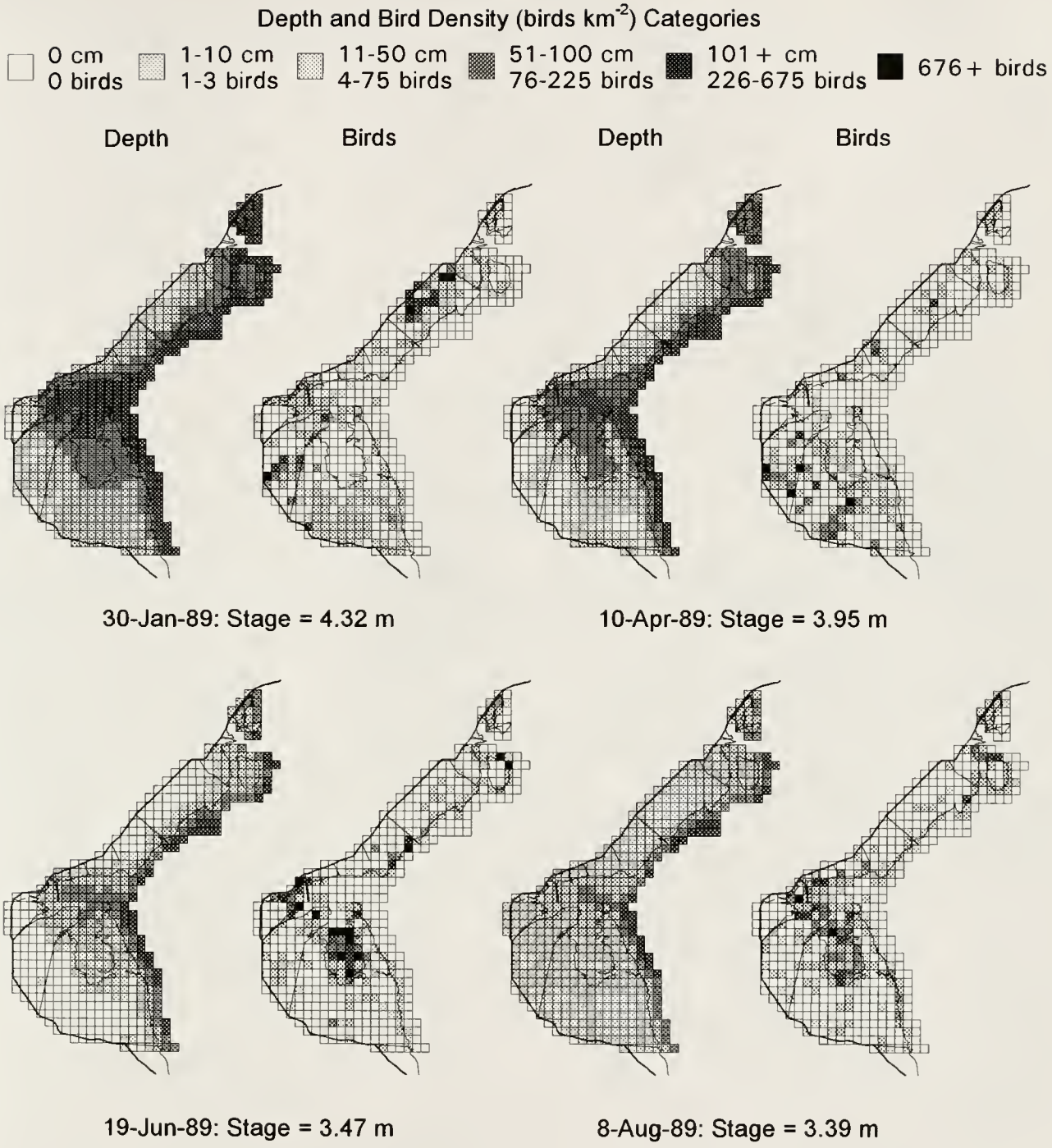


Figure 2-9. Select 1989 combined-species wading bird density maps for the transect and Eagle Bay Island areas, shown in relation to plots of mean water depth derived from the OKEEHYDRO hydrologic model (Richardson and Hamouda 1994).

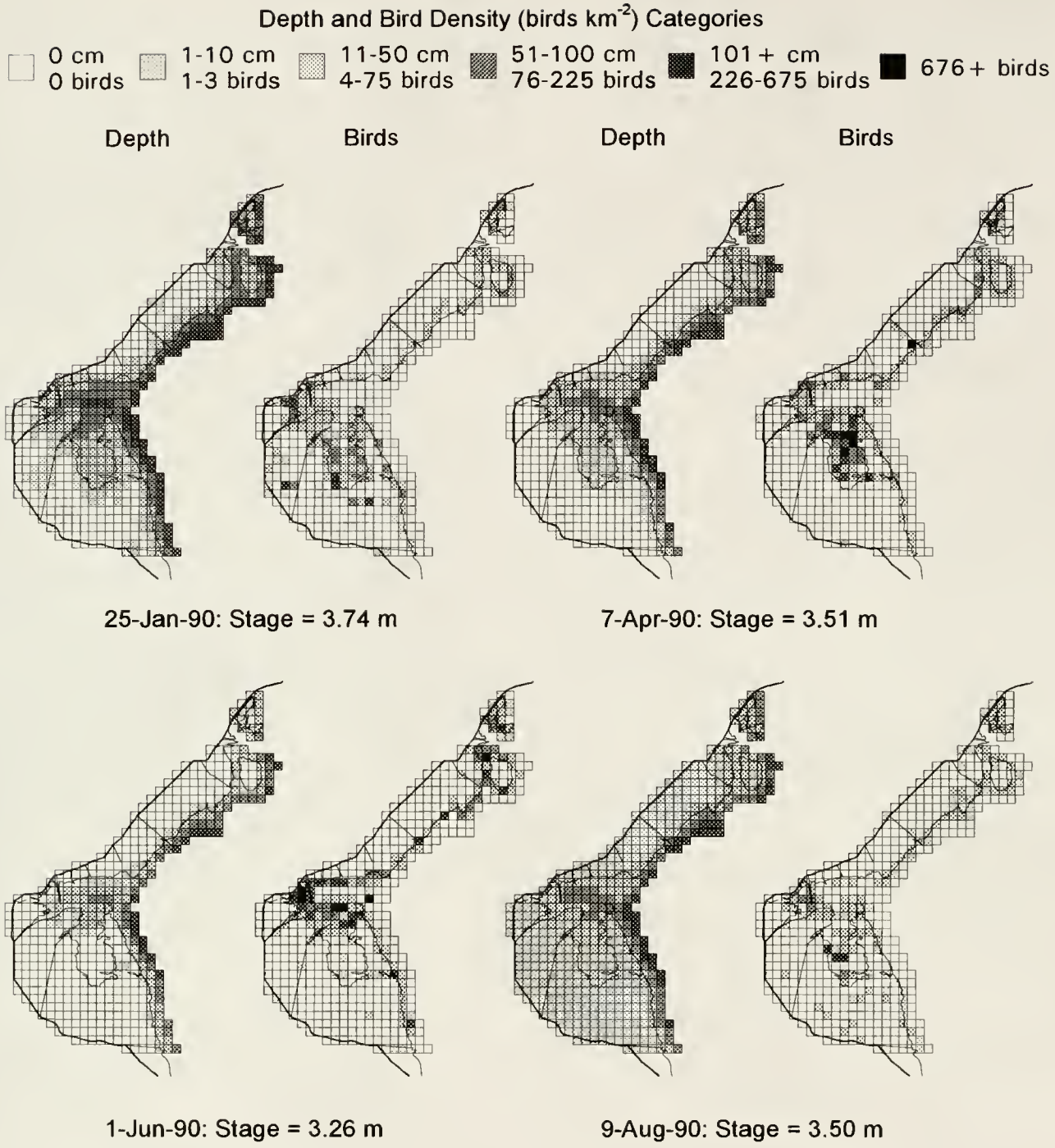


Figure 2-10. Select 1990 combined-species wading bird density maps for the transect and Eagle Bay Island areas, shown in relation to plots of mean water depth derived from the OKEEHYDRO hydrologic model (Richardson and Hamouda 1994).

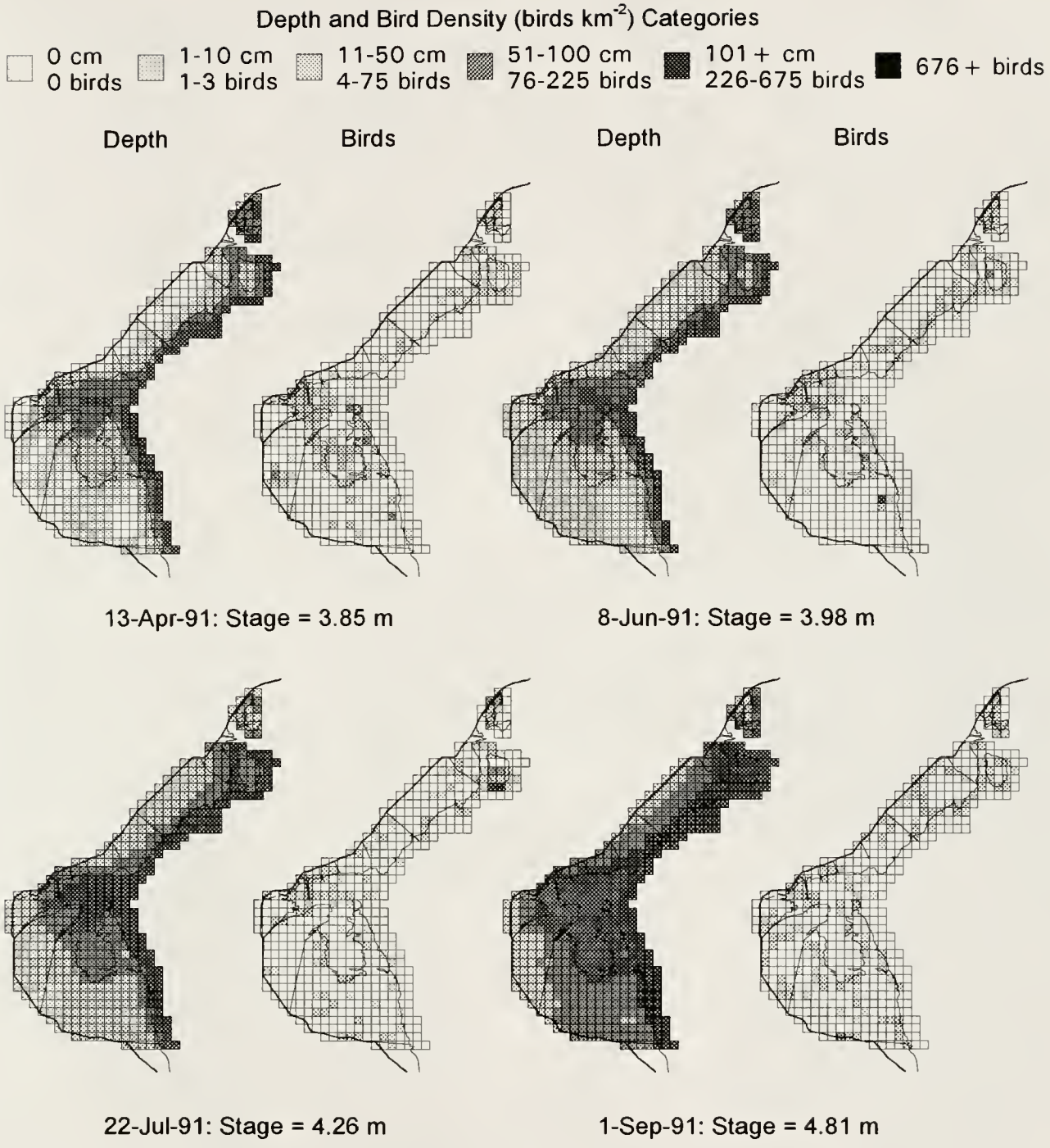


Figure 2-11. Select 1991 combined-species wading bird density maps for the transect and Eagle Bay Island areas, shown in relation to plots of mean water depth derived from the OKEEHYDRO hydrologic model (Richardson and Hamouda 1994).

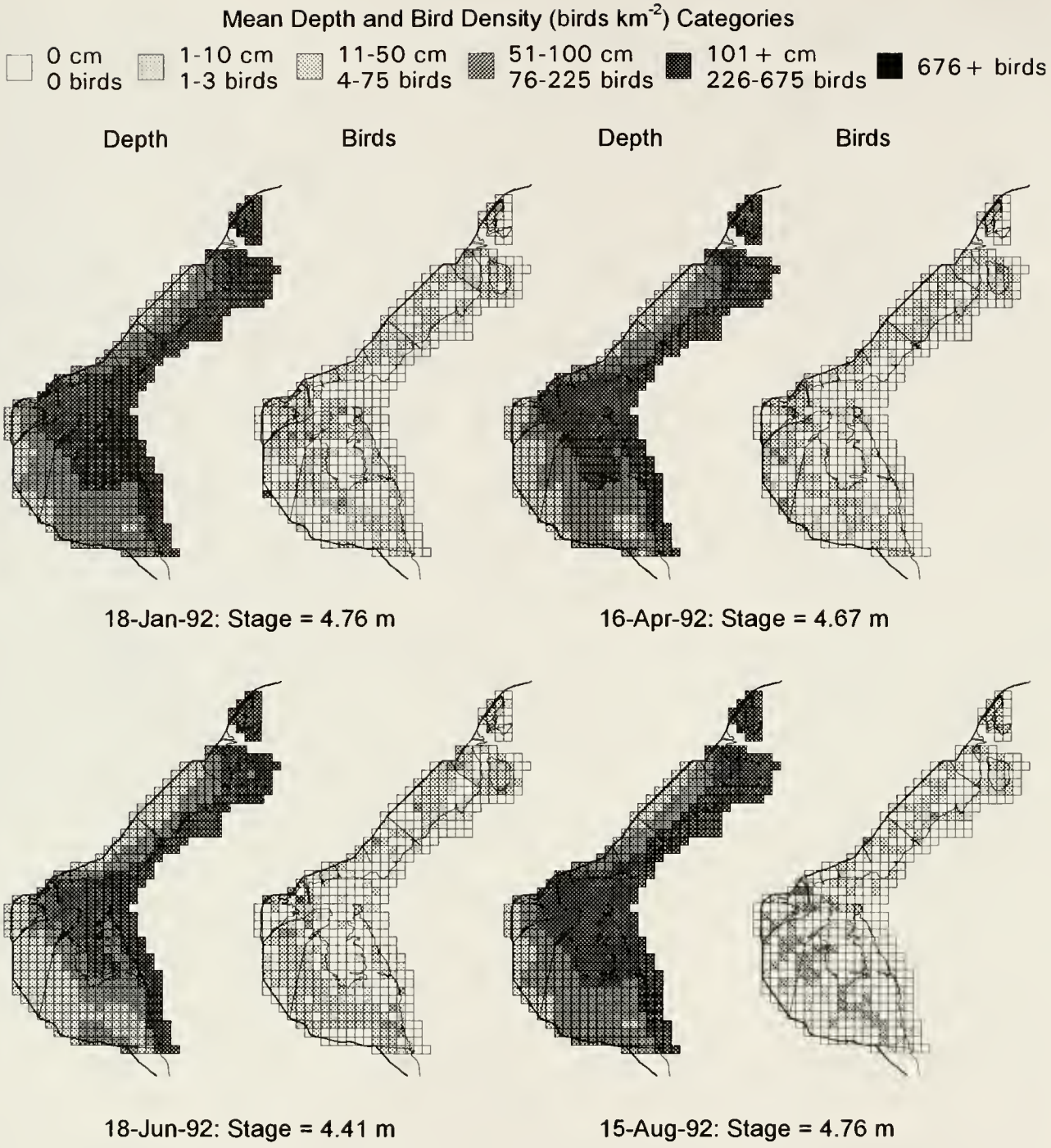


Figure 2-12. Select 1992 combined-species wading bird density maps for the transect and Eagle Bay Island areas, shown in relation to plots of mean water depth derived from the OKEEHYDRO hydrologic model (Richardson and Hamouda 1994).

Airboat trails, which are prevalent on the lake, were conspicuous examples of localized depressions that remained wet and attracted wading birds when most of the surrounding marsh had dried.

With the above exceptions in mind, the maps confirm that the distribution of birds was generally constrained to wet areas with mean water depths below 50 cm. At high lake stages, relatively small numbers of birds were dispersed throughout the higher-elevation, shallower areas of the littoral zone (January 1989, Fig. 2-9; throughout 1992, Fig. 2-12). Habitats commonly used at this time included Panicum-dominated mixed grasses and patches of Eleocharis and Rhynchospora (see vegetation maps introduced in the next section and maps provided in Richardson and Harris [1994] for greater detail). In contrast, the number of birds increased dramatically as the lake stage dropped during the drought periods of 1989 and 1990 (June 1989, Fig. 2-9; April and June 1990, Fig. 2-10). Foraging activity was progressively restricted to the Eleocharis flats of Moonshine Bay, then to mixed lakeward-fringe habitats, and eventually to exposed beds of submerged vegetation and open-water fringes at the lowest lake stages. The 1989 and 1990 maps (Figs. 2-9, 2-10) indicate that areas of concentrated foraging were most often located in either shallow habitats (1-10 cm depths) or areas of transition from shallow to moderate depths (10-50 cm).

The 1991 maps (Fig. 2-11) indicate that, despite generally moderate lake stages, the lack of a spring surface-water recession resulted in sparse, widely dispersed foraging populations. In addition, comparing the last maps in the 1989, 1990, and 1992 series against others in each series confirmed that foraging birds were less common during late surveys when surface-water levels were rising than during early surveys when water levels were declining. This was true despite the fact that areas of suitable depth were equally or more abundant late in the season.

Vegetation Maps and Changes During the Study.

Table 2-1 lists the original classes of vegetation (with scientific nomenclature for those species hereafter referred to by common names) represented on the classified-satellite-image vegetation maps produced by Richardson and Harris (1994). The abbreviated names provided in Table 2-1 are used in Table 2-2 to describe the composition of the FASTCLUS-derived aggregate vegetation classes assigned to each of the survey grid cells. I arrived at the choice of 18 classes by an iterative process. When using the FASTCLUS procedure, one must specify in advance the number of classes desired; I compared the results of specifying between 10 and 27 classes. My goal was to reduce the number of classes as much as possible without eliminating recognizably distinct classes of habitat, particularly those that observations suggested were important for foraging wading birds. I decided that 18 classes achieved the best compromise. If I included more, some classes did not correspond to recognizable assemblages. If I included less, some distinct and important classes were lost.

Justification for listing vegetation types in Table 2-2 that comprised less than 10% cover is based upon observations that small patches of favorable habitat often attracted birds to otherwise seemingly inaccessible habitat complexes (e.g., Polygonum-dominated or Eleocharis and Nymphaea patches in a thick cattail matrix). Even as low as 5% cover potentially equaled a patch size of 50,000 m^2, which could accommodate a sizable flock. Moreover, in many cases I included low-cover types because they represented a closely related extension of major groups (e.g., mixed cattail and Nymphaea [CATNY] relative to cattail [CAT]). The codes chosen to represent each of the final classes therefore reflect primarily dominant constituents, but in some cases I felt it was important to emphasize the inclusion of low-cover categories

Table 2-1. Vegetation types represented on annual, 9.15-m x 9.15-m resolution, classified satellite-image maps produced by Richardson and Harris (1994). Cover statistics for these classes formed the basis for the 1-km x 1-km resolution classification scheme developed to match the wading bird survey grid (see Table 2-2).

Code	Vegetation Type	Code	Vegetation Type
ceph	Cephalanthus occidentalis	open	deeper open water
mela	Melaleuca quinquenervia	peri	periphyton
wil	willow, Salix caroliniana	elper	Eleocharis and periphyton mix
spar	Spartina bakeri	nyel	Nymphaea and Eleocharis mix
cat	cattail, Typha sp.	lot	lotus, Nelumbo lutea
saw	sawgrass, Cladium jamaicensis	subcl	submerged vegetation
mixup	mixed upland complex		and shallow open water
rhy	Rhynchospora tracyi	catny	cattail and Nymphaea mix
bog	Pontedaria lanceolata and	phr	Phragmites communis
	Sagittaria lancifolia mix	maid	maidencane, Panicum
mixgr	mixed grasses, primarily		hemitomon
	Panicum repens	sppan	Spartina and Panicum mix
nym	Nymphaea sp.	sucd	successional-disturbed mix
eleo	Eleocharis celulosa	poly	Polygonum sp.
hyac	hyacinth, Eichhornia crassipes	cpsag	cattail, Pontedaria, and
scrp	Scirpus sp.		Sagittaria mix

Table 2-2 Identification codes and composition of vegetation community classes assigned to 1-km x 1-km survey grid cells for habitat selection analyses (see Table 2-1 for descriptions of constituents).

Code	Mean % Cover of Primary and Important Secondary Constituents					
MU	mixup-58	cat-14	mixgr-8			
MG	mixgr-53	sppa-5	spar-3	cat-18		
SMG	spar-39	mixgr-20	sucd-11	cat-10	catny-4	bog-7
SD	sucd-67	mixgr-10	wil-6			
SCWP	sucd-35	cat-14	catny-4	wil-10	poly-8	
WCNP	wil-44	sucd-19	cat-7	catny-8	poly-6	
CNWP	cat-25	catny-17	nym-5	wil-9	poly-7	
C	cat-58	catny-6	mixgr-6			
ECN	eleo-28	nyel-11	cat-11	sucd-12	saw-5	mixgr-5
E	eleo-54	elper-8	nyel-7	catny-2	cat-8	mixgr-8
EP	elper-39	eleo-18	peri-7	cat-9	mixgr-6	
CSNE	saw-24	cat-24	catny-7	nyel-6	mixgr-8	
MCSE	mela-57	cat-7	saw-7	nyel-7	eleo-5	
RCGE	rhy-26	cat-24	mixgr-12	elper-11	eleo-5	saw-9
L	lot-49	cat-12	open-7	subcl-6		
SUB	subcl-74	open-7				
OSS	open-47	subcl-24	scrp-10	cat-7		
O	open-94					

that appeared important to wading birds. The issue highlights the fact that the 1 km^2 scale of spatial resolution masked some important fine-scale patterns of habitat use. In the following accounts, I point out several instances where I thought this occurred.

The vegetation maps that resulted from the FASTCLUS procedure are shown in Figures 2-13 and 2-14. In the following discussion, I highlight the most prominent and pertinent changes in vegetation communities that occurred during the study. For additional detail, readers should consult Richardson and Harris (1994) and Richardson et al. (1994).

In 1989, cattail (C) dominated a large portion of the survey area. However, in the southwestern section of the transect area, EP (Eleocharis and periphyton), CSNE (cattail and sawgrass with patches of Nymphaea and Eleocharis) and RCGE (Rhynchospora and cattail--and sawgrass--with mixed grass and Eleocharis patches) vegetation mixes were abundant and graded into more pure Eleocharis stands (E) in Moonshine Bay (Fig. 2-13). In the upper Indian Prairie region, mixed grasses (MG) were prevalent and graded into E and EP mixes toward the north and into CNWP mixes (cattail and Nymphaea with patches of willow and Polygonum) toward the lakeward margin. The 1989 map contained relatively few cells classified as dominated by submerged vegetation (SUB). Instead, most outer fringe cells were classified as O (deeper open water) and some as OSS (mixed open water and submerged vegetation with patches of Scirpus). This reflected most closely the conditions prevalent during the first half of the 1989 season, but a slight variation in classification protocol actually under-represented the 'subcl' class on the original maps (Richardson and Harris 1994). The latter had some ramifications for the habitat selection analyses (see below). However, the ensuing drought cycle greatly enhance the spread of submerged vegetation (Zimba et al. 1994), and the indication of greater cover for the SUB habitat

Figure 2-13. One km^2-scale vegetative cover maps for 1989 and 1990 derived from 10-m classified-satellite-image maps produced by Richardson and Harris (1994). See Tables 2-1 and 2-2 for descriptions of vegetation categories. (Note: These are color maps. Individuals who have purchased copies of this dissertation through University Microfilms may request original color copies from the author.)

1990
1989
C
MU
SCWP
EP
L
CSNE
RCGE
SD
SUB
ECN
OSS
E
O
MG
WCNP
MCSE
SMG
CNWP

Figure 2-14. One km^2-scale vegetative cover maps for 1991 and 1992 derived from 10-m classified-satellite-image maps produced by Richardson and Harris (1994). See Tables 2-1 and 2-2 for descriptions of vegetation categories. (Note: These are color maps. Individuals who have purchased copies of this dissertation through University Microfilms may request original color copies from the author.)

1991
1992
C
MU
SCWP
EP
L
CSNE
RCGE
SD
SUB
ECN
OSS
E
O
MG
WCNP
MCSE
SMG
CNWP

type on 1990 and 1991 maps (Figs. 2-13 and 2-14, respectively) would not have been obscured by an adjustment to the 1989 map.

Prior to mid-1989, the main willow-dominated section of Eagle Bay Island (see maps in Richardson and Harris [1994] for best detail) was almost entirely surrounded by open water and sparse submerged vegetation, with a narrow fringe of Scirpus in some areas. As the drought progressed, a wide fringe of Scirpus, cattail, grasses and sedges, Cesbania sp., other annuals, and submerged vegetation began to develop. By 1990 the "island" had effectively doubled in size. In addition, a smaller, previously isolated stand of Scirpus located just offshore of Eagle Bay Island began to expand. Mats of water hyacinth and water lettuce filled open areas, and expanding stands of Scirpus and cattail increased the areal coverage of the new "island". Between these two island regions, an expanse of lotus pushed up through a thickening Hydrilla and Vallisneria understory. This was an important feeding area for nesting adults from Eagle Bay Island and nearby areas (Chapter 3).

In late 1989, a severe freeze struck southern Florida and killed much of the emergent vegetation on the lake; cattail was hit particularly hard (Richardson and Harris 1994). During the following spring and summer, a series of lightning fires were ignited. Most of the marsh was nearly dry due to the drought, and the fires burned very hot and cleared much of the emergent vegetation. In response, a complex mosaic of mostly annual, successional species emerged (Richardson and Harris 1994). As a result, a large portion of the 1990 vegetation map (Fig. 2-13) was assigned to the highly variable successional-disturbed (SD) class, and several more distinct classes were eliminated (i.e., MCSE - Melaleuca forest grading to cattail and sawgrass with Eleocharis and Nymphaea patches, RCGE, CNWP, and most of what was MG). Otherwise, many of the cells in the southwestern section that were classified as E and EP in 1989 shifted in

composition to the more complex ECN class (mixed Eleocharis, cattail, and Nymphaea) in 1990. Moreover, in many areas previously dominated by other species, patches of Polygonum emerged; an expansion of the mixed-successional SCWP class (a complex mix of the SD class and patches of cattail, willow, Polygonum, and other species) reflected this trend.

By 1991, as the lake stage began to increase again, many of the aquatic species regained their former dominance. The Eleocharis stands in the southwestern and Moonshine Bay areas and the mixed-grass complexes on upper Indian Prairie reemerged (Fig. 2-14). In addition, a new class of mixed grasses appeared that included extensive patches of Spartina interspersed with Panicum and other species (SMG). Cattail was slower to regenerate fully; the CNWP class reappeared at 1989 levels, but the heavily mixed SCWP complex--in particular flats of Polygonum--also remained prevalent. The thick submerged beds and floating mats that developed around Fisheating Bay, Eagle Bay Island, and King's Bar continued to thrive, but deepening water reduced accessibility for most wading bird species.

By 1992, cattail had again regained its stronghold on the lake, and the regeneration of Eleocharis and Panicum continued (Fig. 2-14). The exotic Melaleuca also expanded dramatically following the drought/fire cycle. Compared to 1989, by 1992 the number of MCSE cells had doubled along the western margin near Moore Haven and south, generally filling in where the 1989 RCGE habitats once were common. Willow also responded favorably to the drought/rewetting cycle, and the WCNP class (willow-dominated, with patches of cattail grading to Nymphaea, and Polygonum) increased five-fold over 1989 levels. Willow-dominated habitats rarely attracted large numbers of foraging wading birds during this study (see below), but willow serves as the primary nesting substrate for all species (Chapter 4; Zaffke 1984;

David 1994a). During the 1992 season, after the lake stage had returned to high levels, the extensive floating mats and thick Hydrilla beds that flourished during 1990 and 1991 in Fisheating Bay and around Eagle Bay Island and King's Bar thinned and dispersed. This eliminated one of the last remaining profitable foraging habitats on the lake for Snowy Egrets, in particular.

Habitat Selection Analyses

Methodological details, summary graphics, and interpretation of results.

Hydrologic conditions varied each season and patterns of habitat-use changed accordingly. I began by examining selection trends for each survey separately. However, I concluded that early- and late-season combined-survey analyses (i.e., survey data combined for January-April and May-August) were sufficient to represent major intra-annual, hydrologically-related shifts in distribution. I then compared the semiannual results with those derived from annual combinations of data, and culminated the perspective by combining information from all surveys in one analysis. In this progressive fashion, I was able to identify habitat selection trends that persisted across all temporal scales, and to isolate other trends that seemed more related to seasonal or annual hydrologic conditions. As mentioned previously, the annual scale of temporal resolution was most compatible with the vegetation community data. This therefore was the lowest temporal scale for which I calculated χ^2 statistics, and is the focus of attention in the accounts that follow. My presentation of results emphasizes major and consistent study-wide trends, but also specifically highlights where changes in lake stage led to shifts in habitat selection on both intra- and inter-annual scales.

Species-specific graphical representations of the annual χ^2 test results for 1989-1992 are provided in Figures 2-15 - 2-18. The bars in the figures represent percent

deviations from expected (relative to abundance of vegetation types) of bird counts summed by vegetation type across each series of annual surveys (i.e., not counts of distinct individuals):

plotted value = (total count in given vegetation type / grand total count of birds)
- (number of cells of a given vegetation type / total number of cells)

Bars extending above zero indicate higher-than-expected-use or positive selection of the vegetation type (for practical purposes no maximum limit), whereas those extending below zero indicate underutilization or negative selection (limit = -100%; i.e., maximum underutilization or no use). All future references to "active" or significant, positive or negative selection will imply χ^2 $P < 0.001$. Similarly, reference to marginal selection will imply $0.001 < P < 0.05$, and to neutral selection $P > 0.05$. I discuss the reasons for choosing a conservative significance level in the discussion section.

A two-part alphanumeric code appears above each bar in Figures 2-15 - 2-18. The first half of the code is a number between 0 and 10 that indicates on a relative scale how many birds used each vegetation type during the specified year. For each wading bird species, I summed the survey counts within vegetation types and years, and then divided each total by the number of surveys conducted during the given year. This resulted in estimates of the average number of each species counted in each vegetation type on a typical survey in a given year. For each species, I pooled the estimates for all vegetation types and all years, and from these I identified the study-wide maximum value and to it assigned the value of 10 or 100%. I scaled all other estimates accordingly in 10% increments with 0 = no birds, 1 = 1-10% of the maximum, 2 = 11-20%, etc. The numeric codes therefore reflect study-wide trends in concentration of numbers in specific types of vegetation, without regard for the

abundance of vegetation types. Thus, they provide a means for judging the comparative importance of the indicated annual selection trends. The second half of the code is a label and is absent in most cases, indicating a significant χ^2 test ($P < 0.001$). Otherwise, a "?" indicates marginal significance and an "n" indicates no significant difference ($P > 0.05$).

To properly interpret the results of the habitat selection analyses, one must always keep in mind that the analyses did not statistically account for the interactive effects of water depth and vegetative cover. Thus, although the label for a given habitat type remained consistent, and the species of vegetation occupying a given cell may have remained relatively consistent, the hydrologic characteristics of the cells were always changing. In many cases, the classification of cells changed over the course of the study because hydrologic conditions varied enough to cause large-scale shifts in the vegetation. However, in some cases a change in the use of a given cell by birds occurred even though the classification of the cell did not. Such a change could have occurred because more favorable vegetation mixes emerged in nearby areas. However, the change could also have occurred because the particular parcel of habitat either dried out or flooded too deeply for it to remain an attractive foraging area. Generally low use of upper-elevation marsh habitats at low lake stages undoubtedly had more to do with the area being dry than with other types of vegetation being more attractive. Conversely, typically few birds used submerged vegetation and open-water habitats at high lake stages because the water was too deep for wading, not because prey were absent or some feature of the vegetation was unattractive.

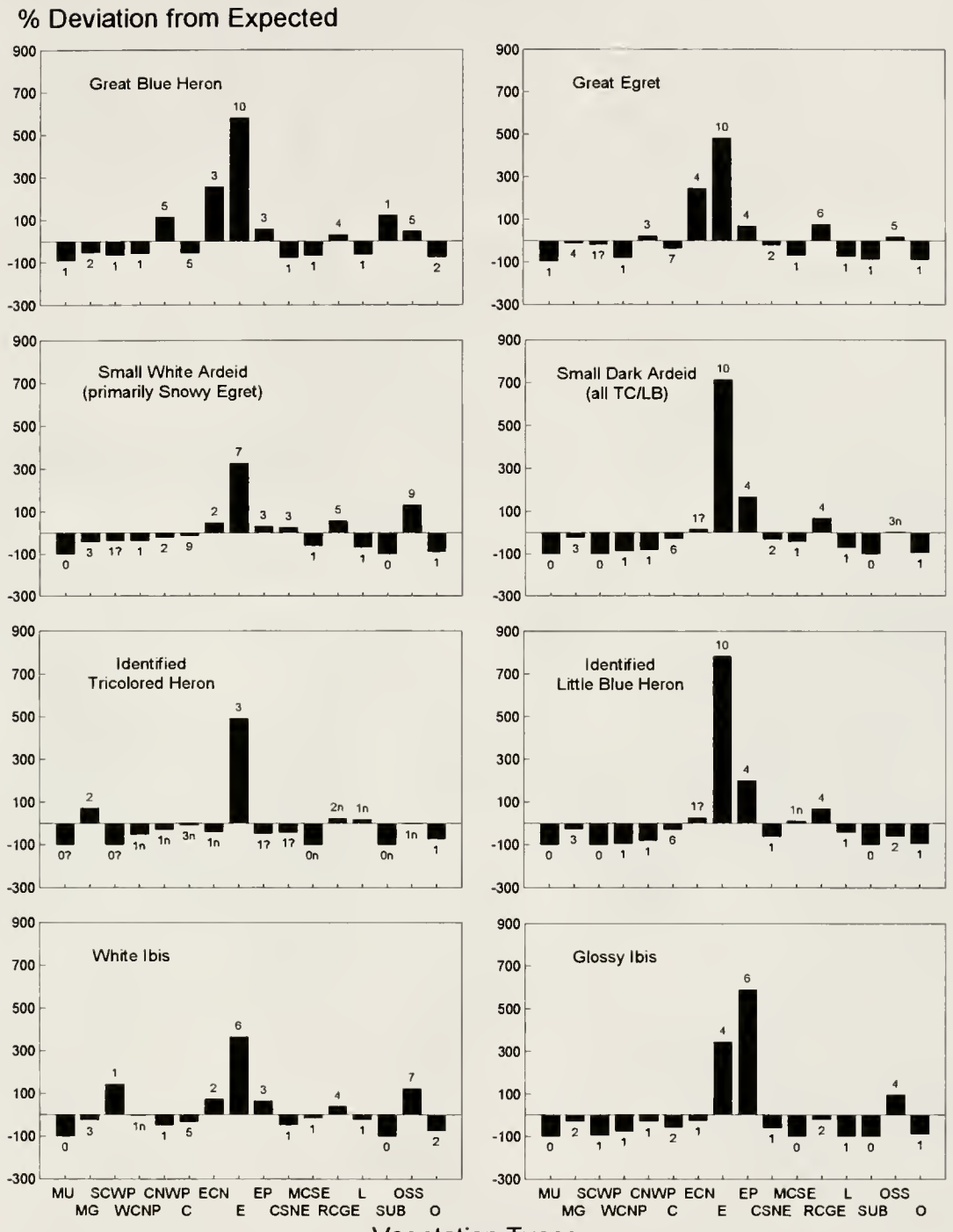


Figure 2-15. Wading bird foraging habitat selection in relation to vegetation assemblages in 1989; Chi-square tests of independence with bird densities summed across surveys. Vegetation codes are described in Table 2-2. Alphanumeric codes above bars are interpreted as follows: number = study-wide relative amount of use, 10 highest--see text for details; label = Chi-square significance--n = $P > 0.05$, ? = $0.001 < P < 0.05$, no label = $P < 0.001$.

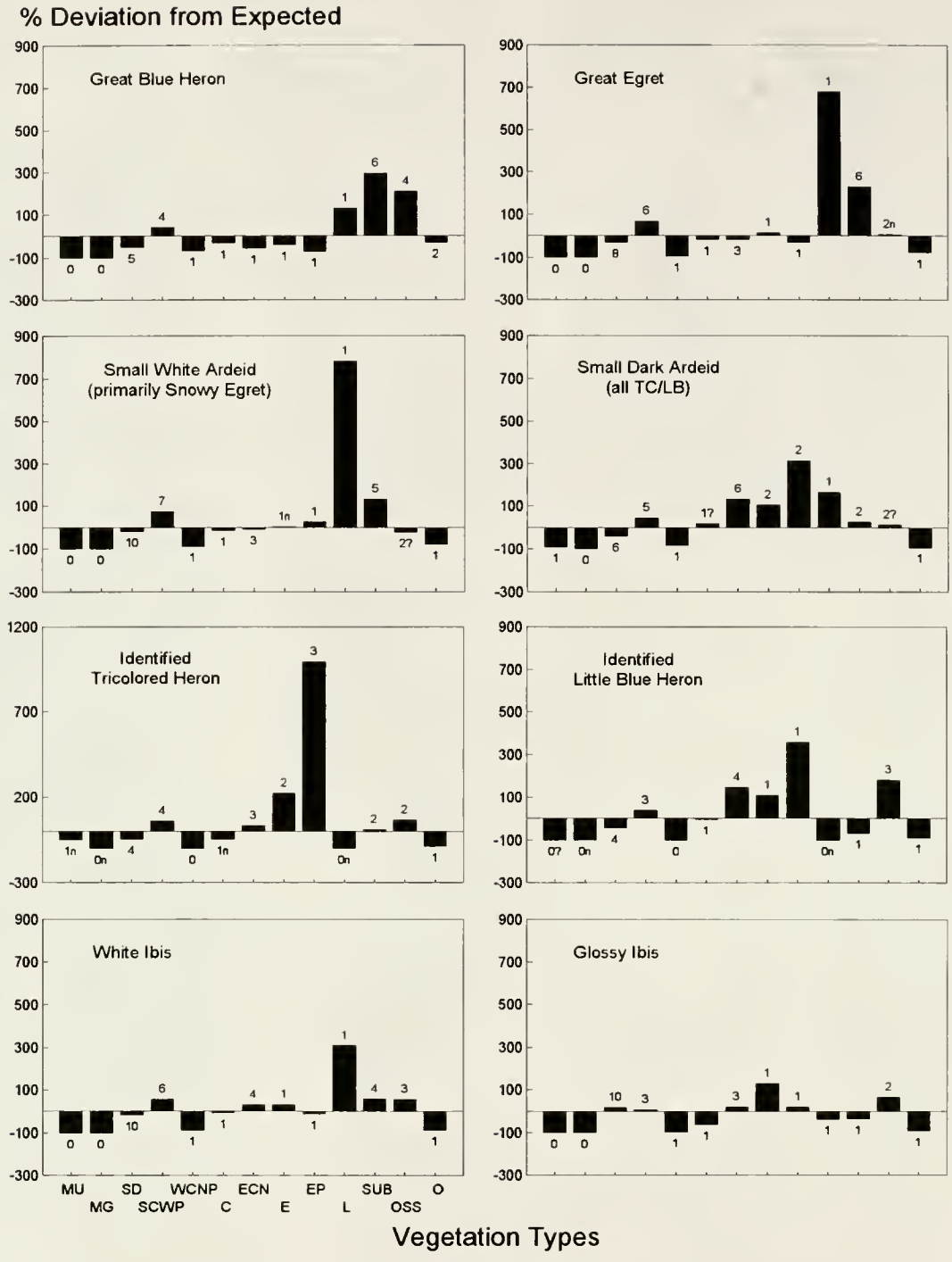


Figure 2-16. Wading bird foraging habitat selection in relation to vegetation assemblages in 1990; Chi-square tests of independence with bird densities summed across surveys. Vegetation codes are described in Table 2-2. Alphanumeric codes above bars are interpreted as follows: number = study-wide relative amount of use, 10 highest--see text for details; label = Chi-square significance--n = P > 0.05, ? = 0.001 < P < 0.05, no label = P < 0.001.

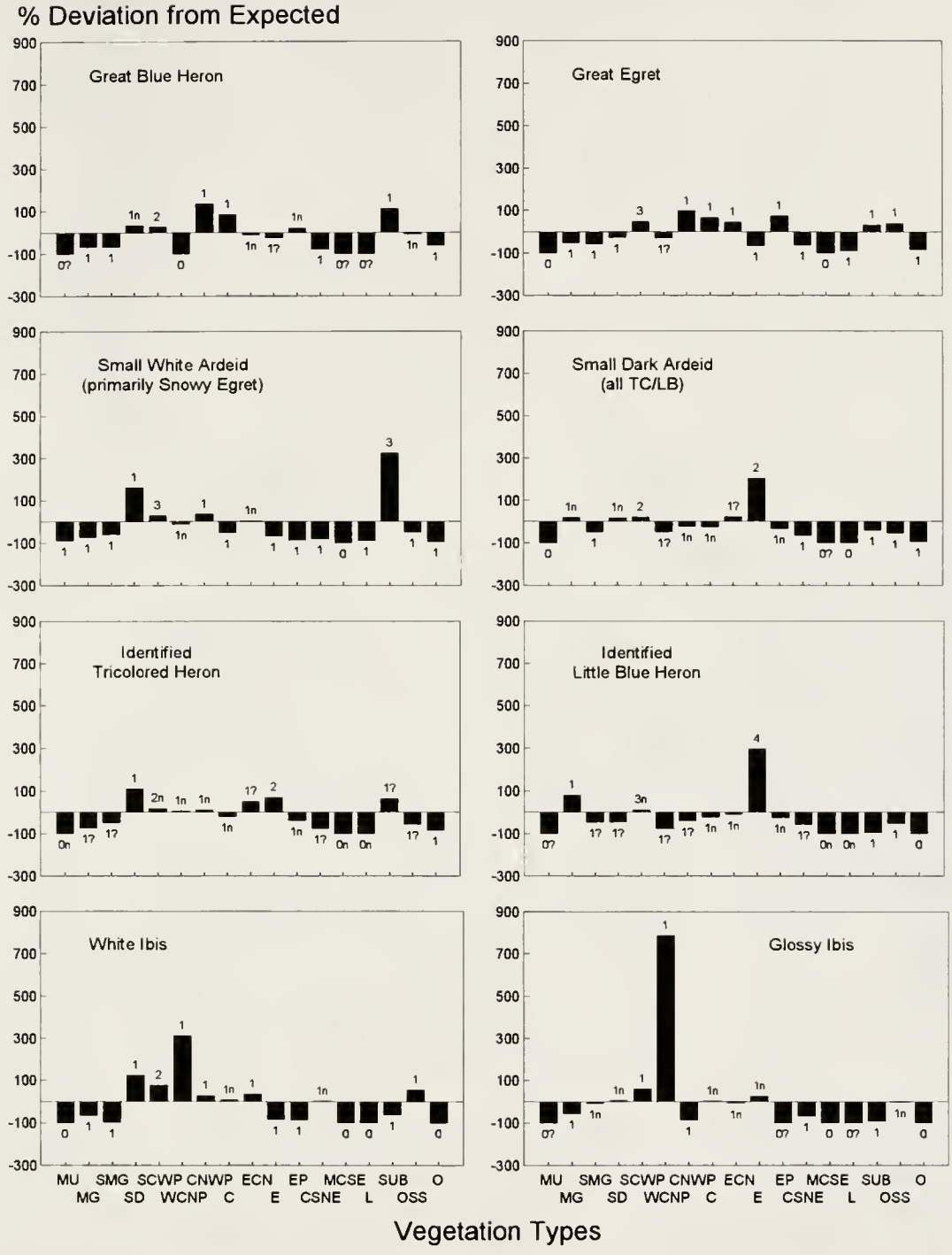


Figure 2-17. Wading bird foraging habitat selection in relation to vegetation assemblages in 1991; Chi-square tests of independence with bird densities summed across surveys. Vegetation codes are described in Table 2-2. Alphanumeric codes above bars are interpreted as follows: number = study-wide relative amount of use, 10 highest--see text for details; label = Chi-square significance--n = P > 0.05, ? = 0.001 < P < 0.05, no label = P < 0.001.

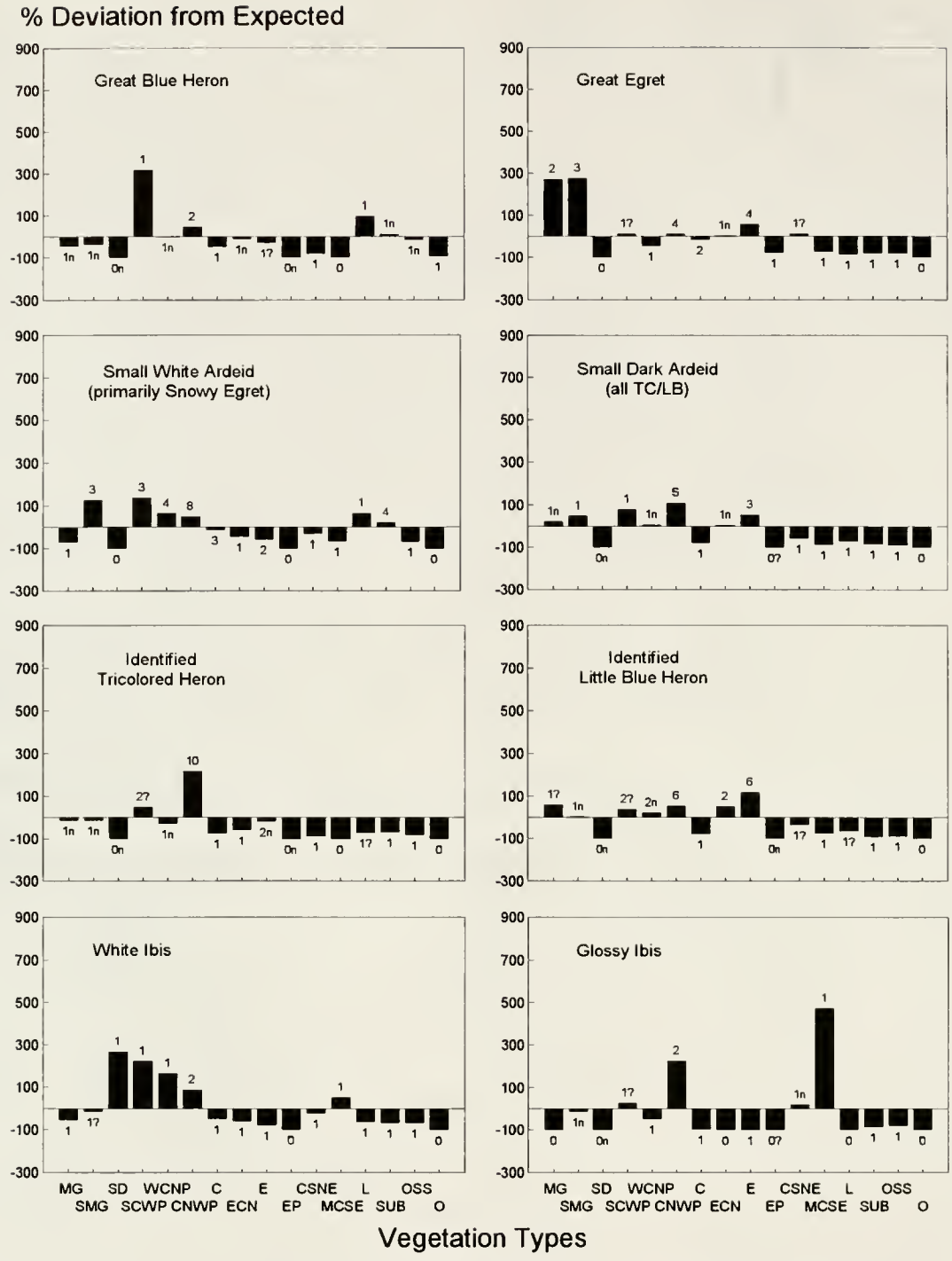


Figure 2-18. Wading bird foraging habitat selection in relation to vegetation assemblages in 1992; Chi-square tests of independence with bird densities summed across surveys. Vegetation codes are described in Table 2-2. Aplhanumeric codes above bars are interpreted as follows: number = study-wide relative amount of use, 10 highest--see text for details; label = Chi-square significance--n = P > 0.05, ? = 0.001 < P < 0.05, no label = P < 0.001.

Habitat selection trends. All species selected wet-prairie habitats of moderate structural complexity, particularly those featuring Eleocharis (E, EP, and often ECN), during some portion of most years (Figs. 2-15 - 2-18). The only exceptions were that Snowy Egrets (SWA) and both species of ibis underutilized these habitats in 1992 (Fig. 2-18). The largest extent of Eleocharis habitat occurred in and around the fringes of Moonshine Bay. This region and a less extensive but more diverse area on northern Indian Prairie were the focal points of foraging activity at moderate lake stages (3.7-4.3 m) during 1989 and the first half of 1990 (Figs. 2-9, 2-10). Most species used and actively selected structurally similar RCGE habitats more at higher lake stages early in 1989. The center of distribution for RCGE habitats was west and south of the large Moore Haven nesting colony (shown in Fig. 2-1 due north of the town of Moore Haven). The close proximity of RCGE habitats to the colony may have enhanced their attractiveness. The same relationship may have applied in 1992. The Moore Haven colony was essentially unused in 1990 and 1991, but was reoccupied in 1992 when water levels rose again (Chapter 4). The RCGE class was not represented as such after 1989 due to the invasion of Melaleuca and other changes. However, in 1992 the area still included patches of Eleocharis, Rhynchospora and grasses, and selection by both species of ibis of the MCSE habitat type reflected a return to the area (Fig. 2-18 and Fig. 2-12: April/June 1992). The change in classification resulted from changes in the vegetative community, but this is one case where the 1 km^2 scale of resolution failed to capture some important fine-scale details concerning patch choice. Zaffke (1984) also commented on the importance of this southwestern region and these habitat types at higher lake stages. In general, however, selection of Eleocharis habitats was more irregular during 1991 and 1992 (Figs. 2-17, 2-18), as Moonshine Bay reflooded deeply enough to exclude most species (Figs. 2-11, 2-12). Throughout the

study, Great Egrets remained the most consistent in their selection of E and EP habitats, with Little Blue Herons ranking second in overall consistency and strength of preference.

Most of the higher-elevation prairies and even the Eleocharis flats of Moonshine Bay dried out when the drought reached its peak in mid-1990. Most the remaining aquatic foraging habitat was restricted to beds of submerged vegetation and lotus, and to open flats in bays and along the lakeward fringes of the littoral zone. As noted above, the largest populations of foraging birds observed during the study were attracted to the lake at this time. Activity was focused primarily in mixed submerged habitats (SUB, OSS, and adjacent lotus [L] flats), mostly in Fisheating Bay and around King's Bar and Eagle Bay Island (Fig. 2-10; June 1990). Relatively large numbers of all species actively selected these habitats during the second halves of the 1989 and 1990 seasons (least true for Tricolored and Little Blue herons, which remained more dedicated to E and EP habitats). Snowy Egrets and Great Blue Herons exhibited the strongest, most consistent tendency to select submerged habitats, but Great Egrets also exhibited a high affinity for submerged (SUB) and nearby mixed lotus and Hydrilla flats (L) in 1990 (Fig. 2-16). Observations revealed that Snowy Egrets were attracted by floating mats of water hyacinth and the large surface leaves of lotus (strong selection for L habitats in 1990, Fig. 2-16). Both provided support in deep water (also see Murdich 1978) and facilitated aerial foraging over prey-rich Hydrilla beds. Snowy Egrets continued to use these habitats and herbicided mats of water hyacinth (see below) well into 1992 after most other species had moved back toward the higher-elevation marshes. Great Blue Herons typically focused more on open areas (O) and open pockets in submerged beds (OSS) occupied by breeding sunfish (Lepomis sp.) and largemouth bass (Micropterus salmoides). This trend was most notably manifest

as atypical, near-neutral selection of the most open habitat types (O) in 1989 and especially 1990 (Figs. 2-15, 2-16). The relative density of Great Blue Herons in these habitats was also atypically high during these times.

Ibises shifted back to MCSE habitats on the southwestern margin once surface-water levels rose again following the 1989/90 drought. However, all other species shifted their attention more to the mixed-transitional SCWP, CNWP, WCNP and less often SD habitats (all of which flourished following the drought), and to the higher-elevation MG and SMG habitats on Indian Prairie. Mixes of Eleocharis and Rhynchospora often occurred in the first group of transitional habitat types, but patches of Polygonum attracted equal or greater activity. Great Egrets were particularly attracted to reflooded Panicum-dominated mixed grass habitats in 1992 (Fig. 2-18). Most species actively selected SCWP habitats and used them heavily throughout the 1990-1992 seasons; however, in 1989 this habitat type was uncommon and only White Ibises showed positive selection (Figs. 2-15 - 2-18). CNWP and WCNP habitats were used less consistently. Use of these habitats was generally low during the 1989 and 1990 drought periods (Figs. 2-15, 2-16), but was higher among Great Blue Herons and Great Egrets early in 1989 (Fig. 2-15), and was higher among most species--especially ibises--in 1991 and 1992 after the areas were reflooded (lake stages above 3.7 m; Figs. 2-17, 2-18).

The SD class of highly disturbed habitats attracted large numbers of birds in 1990. However, this habitat class was ubiquitous and represented a wide array of mixed-transitional assemblages, and selection was generally neutral or negative (Fig. 2-16). Glossy Ibises were the notable exception, suggesting that the species was strongly attracted to diverse mixes of vegetation and/or areas of decaying vegetation (the latter may support high invertebrate populations). There may have been more

statistical evidence that Glossy Ibises selected such habitats in 1990, but my observations suggested that White Ibises were also attracted to areas of decaying vegetation and transitional complexes. The species' near-neutral selection of SD habitats in 1990 lent support for this contention (Fig. 2-16). Snowy Egrets also used SD habitats heavily in 1990, with selection near neutral (Fig. 2-16). Moreover, White Ibises, Snowy Egrets, and identified Tricolored Herons all showed significant positive selection for SD habitats in 1991, after a significant amount of habitat regeneration had occurred and the number of SD cells had declined. Thus, it appeared that, like Glossy Ibises, these species were attracted to diverse mixes of vegetation. Both species of ibis also actively selected willow-dominated WCNP habitats in 1991, habitats that included mixtures of muddy, coarse detritus and transitional vegetation interspersed with the willows. There was only one cell classified as SD in 1992, and only one group of 50 White Ibis occurred there. However, because White Ibises were uncommon in 1992, the observation contributed to an overall significant positive selection trend (Fig. 2-18). The validity of the significance test was questionable, however, because the expected frequency was so low.

Cells classified as dominated by cattail (C) were also heavily used, but as with SD habitats, selection was usually neutral or negative (Figs. 2-15 - 2-18). Cattail was most prevalent in 1989 before the freezes and fires of 1990 removed most of the thick cover, and the volume of use was also highest in 1989. My observations suggested that dense stands of cattail were rarely used by foraging birds; cattail simply had invaded most areas of the lake and was mixed in with almost every other species of vegetation (Richardson and Harris 1994). This is another example where the 1 km^2 scale of spatial resolution masked finer-scale details of habitat use; birds observed near thick cattail (or sawgrass or willow or Phragmites or Melaleuca, etc.) were usually

foraging in smaller patches of less dense habitat (e.g., patches of Eleocharis, Rhynchospora, Panicum, Nymphaea, and Polygonum, or often in airboat trails). At times in 1990/91, however, White Ibises were attracted to thick, decaying mats of cattail, perhaps to feed on large numbers of detritivorous insects and snails.

All 18 classes of vegetation were used for foraging by at least one bird sometime during the study. The MU class was the rarest--one upland area just south and west of the Fisheating Creek inlet (maximum 7 cells in 1989; Fig. 2-13)--and was rarely used, as expected. The densest (SMG and CSNE), most wooded (WCNP and MCSE), and most open (O) habitats also all failed to draw significant study-wide positive selection. However, each of these habitat types attracted at least moderate numbers of some species and positive selection (except for O habitats) by one or more species during at least one half-season. MCSE habitats were the rarest of the group and attracted the second lowest number of birds overall. Nonetheless, the Eleocharis and grass/sedge habitats at the fringes of thicker Melaleuca and cattail/sawgrass stands along the western margin were strongly selected by Little Blue Herons early in 1989 and by ibises in 1992 when the lake stage was high. L habitats were also about as rare as MCSE, but attracted overall strong positive selection by Snowy Egrets, moderately positive selection by White Ibises, and overall neutral but slightly positive selection by Great Egrets. The proximity of lotus stands and submerged beds, particularly Hydrilla, may have caused a spill-over effect and contributed to the apparent but possibly coincidental selection of L habitats. However, Snowy Egrets and cryptic and poorly documented Tricolored Herons regularly used the large, surface leaves of lotus plants for support while foraging around the edges in thick but less supportive Hydrilla. Open water habitats (O) were never actively selected by a species, but most species used O cells to some degree at low lake stages--Great Egrets, Great

Blue Herons, Snowy Egrets, and White Ibises, in particular. Selection approached neutral for both Great Blue Herons and Great Egrets at the height of the drought in late 1990. At this time, large aggregations of birds often collected in totally open areas, apparently to feed on schooling fishes and breeding sunfish.

The southern island and marsh areas along the East-South Route (Fig. 2-2) included some unique patches of exotic vegetation and altered landscape, but most of the habitats used by foraging birds in these areas were well-represented in the transect and Eagle Bay Island regions. However, an important component of Great Blue Heron foraging habitat covered by the East-South Route was not included in the transect and Eagle Bay Island areas. On most surveys, a substantial proportion (5-20%) of the Great Blue Herons occurred along the open eastern fringe of the lake between Taylor Creek and Pahokee (Fig. 2-1). Many of these birds were fishing from rocks in open water at the edge of the lake; others waded beyond narrow fringes of Scirpus. In some instances, over 100 birds were spaced at intervals of 50-150 m along considerable stretches of "beach". Moreover, nearly all the Great White Herons I observed on the lake were foraging in the same rocky-fringe habitat. The birds' targets probably included large shad (Dorosoma sp.), golden shiners (Notemigonus crystoleuca), sunfish, and possibly occasional schools of mullet (Mugil cephalus).

In summary, seven primary themes or patterns emerged from the habitat selection analyses:

1) Habitats that included Eleocharis figured prominently and most consistently in the selection preferences of all species. Nymphaea, Panicum, cattail, and periphyton were common additional elements. This trend suggested that emergent vegetation of moderate stature and habitats of moderate structural complexity were important to foraging wading birds.

2) Rhynchospora, Eleocharis, and grassy patches fringing the southwestern Melaleuca and cattail/sawgrass stands provided important foraging habitat at lake stages above 4.3 m in 1989--particularly for Little Blue Herons--and in 1992--particularly for ibises.

3) Mixed-grass habitats dominated by Panicum repens on Indian Prairie attracted relatively large numbers of all species in early 1989 with lake stages above 4.3 m. The reflooding of these habitats in 1992 drew strong positive selection from Great and Snowy Egrets.

4) In 1991 and 1992, successional habitat complexes such as SCWP, CNWP, WCNP, and SD--most of which emerged in the wake of the drought and fires--were heavily used, but rarely elicited positive selection. Smaller patches of Polygonum and those featuring diverse, mixed-stature assemblages were the primary attractors in these habitat matrices. Ibises were also attracted to areas of decaying vegetation, perhaps in response to high invertebrate populations.

5) Habitats dominated by cattail also ranked high in terms of volume of use, but usually did not elicit positive selection. Again, thick cattail (and thick sawgrass) was not the focus of attention; instead, interspersed patches of Eleocharis, Nymphaea, grasses, and Polygonum were the real attractors.

6) Although selection preferences varied through the study and attraction to inter-mixed patches of preferred vegetation sometimes led to positive selection, the most heavily wooded habitats--willow dominated WCNP and Melaleuca-dominated MCSE--were usually underutilized relative to their abundance.

7) Habitats dominated by submerged vegetation ranked high in overall selection preference. Maximum attraction occurred when the lake stage was low, but Snowy Egrets, in particular, foraged over deep-water submerged vegetation habitats by

using floating mats for support and by using aerial foraging techniques. Overall, Tricolored and Little Blue herons showed the weakest selection for submerged habitats. The most open lakeward-fringe habitats were always underutilized, but selection approached neutral among the larger species at the lowest lake stages.

General Discussion and Conclusions

Analytical Caveats

The habitat selection analyses could have been improved in several ways. First, it would have been ideal to have vegetation maps that corresponded to each individual bird survey, rather than just annual maps. The annual maps did not adequately represent intra-seasonal changes in vegetation communities that occurred in response to the drought, freezes, and fires. Unfortunately, the cost of the satellite images and the processing time necessary to produce bimonthly maps were unreasonable. Second, a finer spatial-scale of resolution for bird counts, that matched the resolution of the vegetation maps, would have been preferable. However, this would have been feasible over only a very restricted area, and I was primarily interested in documenting macro- rather than microscale patterns of distribution. Third, reclassifying a classified image--i.e., using FASTCLUS to aggregate the original classes of vegetation--might have introduced unnecessary biases such as shifted transition zones and hodgepodge assemblages. It might have been better to classify the raw satellite images at a spatial scale more compatible with the bird data, but the pixels in the images and my survey grid cells still would not have been properly aligned. Thus, many of the survey grid cells would still have enclosed more than one type of vegetation, and some degree of reclassification would still have been necessary.

Furthermore, the original classification was carried out by colleagues with other goals in mind besides wading bird analyses (see Richardson and Hamouda 1994, Richardson and Harris 1994, and Richardson et al. 1994). Regardless, I believe that visual comparisons of the FASTCLUS derived vegetation maps (Figs. 2-13, 2-14) and the original classified satellite maps shown in Richardson and Harris (1994) reveal little reason to question the appropriateness of the former. The important limitation to acknowledge, however, is that the coarse spatial scale of the bird and vegetation maps and the coarse temporal scale of the vegetation maps did obscure fine-scale details of habitat selection. In the results section I pointed out several specific instances where I felt important trends were so obscured, and I emphasize that readers should not draw strong conclusions about implied associations with individual plant species. Instead, readers should focus on implications related to the coarse-scale structural characteristics of the various vegetation assemblages.

A more important issue, is that habitat selection responses are simultaneously functions of both hydrology and habitat structure. Therefore, analyses should account for the interactive effects of hydrology and vegetation types. I first attempted to employ log-linear models to analyze the interactive effects of grid-cell-level hydrology (data derived from the OKEEHYDRO model; Richardson and Hamouda 1994) and vegetative cover on the distribution of birds, in much the same way Hoffman et al. (1994) did for their Everglades data. Unfortunately, even with 507 cells I was unable to retain a reasonable number of vegetation, bird-density and water-depth categories and still produce a dense enough data matrix to render an estimable model. In other words, there were too many combinations associated with too few non-zero bird counts. Thus, for purposes of this manuscript I was forced to consider hydrology and vegetation separately.

The systematic and repetitive nature of my transect sampling scheme presents a possible conflict with a primary assumption of most parametric statistical tests; i.e., the value of any individual observation must be independent of all other such values. It is possible that some spatial correlation structure exists in the cell-based data that least-squares analyses might not adequately account for. Similarly, when I extended the analyses across multiple surveys, a temporal correlation structure might have arisen. The flocks I observed on the lake typically covered much less than a 1 km^2 area, and the spatial resolution of the surveys probably surpassed most birds' frame of reference relative to selecting specific patches of foraging habitat. Moreover, while patterns of habitat use definitely shifted within seasons, the available vegetation maps did not. Accordingly, annual bird abundance datasets were most appropriate. Thus, for purposes of developing this manuscript, I explicitly ignored potential spatial or temporal correlation problems. However, to insure conservative interpretations, I used only simple χ^2 tests of independence to establish the significance of observed habitat selection trends, and I considered only those cases with χ^2 $P < 0.001$ as truly significant.

I am proceeding with a more complex analysis that incorporates fully integrated sets of hydrologic and vegetation data, and explicitly accounts for potential spatial and temporal correlations. This manuscript therefore represents the results of employing relatively straightforward, standard graphical and statistical techniques to analyze the patterns of habitat selection observed during the study, and will serve as a template against which I will compare the results of the more complex statistical approach.

Foraging Habitat Selection

Hydrologic influences. Clearly, hydrodynamics play a dominant role in determining the distribution, accessibility, and quality of foraging habitat available to wading birds around the lake, as well as in other regions (Kushlan et al. 1975; Browder 1976; Ogden et al. 1980; Kushlan 1986a; Powell 1987; Bancroft et al. 1990). Hydrologic trends influence wading bird foraging by imposing limits to accessibility in the form of deep-water and no-water extremes. At lake stages above about 4.6 m, the lake is one continuous pool and little habitat is available to foraging birds. At the other extreme, with lake stages below about 3.7 m, most of the emergent littoral zone dries out and foraging is restricted to a limited but highly productive portion of the lake consisting of outer-fringe mixes of Panicum hemitomon, cattail and Scirpus, lotus and Nymphaea, and particularly submerged vegetation. Within these limits, the pattern of surface-water fluctuation influences prey density and therefore wading bird foraging efficiency (Kushlan et al. 1975; Kushlan 1976a, b, 1979, 1986a; Frederick and Spalding 1994). The unique feature of the lacustrine Lake Okeechobee ecosystem is that during even severe droughts, water and productive beds of submerged vegetation remain and can support prey organisms and foraging birds at a time when most of the surrounding palustrine systems cease to provide quality foraging habitat.

Hydroperiod is another aspect of hydrology that affects wading birds. The productivity of important prey species depends on a sufficiently long hydroperiod (Loftus et al. 1990; Loftus and Eklund 1994). Hydroperiod also determines the distribution and health of vegetation communities (Pesnell and Brown 1977; Richardson et al. 1994), which influences the distribution of prey (Chick and McIvor 1994), the structure and therefore accessibility of foraging habitats, and the distribution and health of willow, the primary nesting substrate (David 1994a). The habitat selection data

presented here suggested that at least some species were attracted to areas featuring complex mixes of vegetation. Seasonal water level fluctuations and interannual differences in hydropattern, combined with periodic large-scale disturbances such as fires and freezes, may ensure the development of diverse arrays of vegetation (Gunderson 1994) and thus provide a wide variety of foraging opportunities for wading birds.

Preference for emergent vegetation of moderate stature and structural complexity. When presented with a choice of foraging habitats at moderate lake stages, all species considered in this study tended to select patches of emergent vegetation of moderate stature and species/structural diversity. Eleocharis-mix habitats, particularly around and in Moonshine Bay and on northwestern Indian Prairie, were consistently selected by most species. Rhynchospora-dominated and mixed-grass (primarily Panicum) habitats in higher-elevation areas attracted more birds at higher lake stages (e.g., above 4.3 m). Flats of Polygonum proliferated in the wake of the freeze-drought-fire cycle and attracted much foraging activity from 1990 onward. Nymphaea and sparse to moderate density cattail were common additions to the preferred mixtures. In contrast, all species generally avoided or underutilized densely wooded or shrubby habitats and dense stands of tall emergents like cattail and sawgrass. The analyses occasionally indicated selection for cattail/sawgrass (C, CSNE), willow-dominated (WCNP), or Melaleuca-dominated (MCSE) habitats, but the 1 km^2 scale of resolution obscured the fact that the patches of habitat actually chosen rarely included the areas where these species occurred in dense stands. These results are generally consistent with information gathered on the lake by Zaffke (1984) from 1977-1981. Nearly 50% of all the White Ibises, Great Egrets, and Snowy Egrets counted were foraging in Eleocharis or Rhynchospora-dominated habitats at moderate

lake stages. Mixed-grass habitats were used more at higher lake stages and accounted for the second highest volume of use. Zaffke also noted that submerged beds were used heavily during 1981 when a drought occurred and the stage dropped to near 3.0 m. Throughout his study, habitats dominated by thick cattail, willow, and Cephalanthus were used comparatively little.

Collopy and Jelks (1989) documented patterns of habitat use for some of the same species (Great Blue Heron, Great Egret, White Ibis) in a matrix of mixed riparian, open-pocket, and forested wetlands in Sarasota County, Florida. They also found that all species tended to forage in wetlands featuring either emergent species of moderate stature and density such as Panicum and Rhynchospora, Pontedaria and Sagittaria, and Polygonum, or floating emergents such as Nymphaea, Nymphoides, and water hyacinth. Conversely, all species tended to avoid woody habitats and dense stands of sawgrass and Hypericum. Hoffman et al. (1994) studied the distribution of the same species in the Everglades and adjacent areas. Their data were resolved to a coarser 4 km^2 spatial scale and they considered only five classes of vegetation. Nonetheless, their results also generally concur with those of this study. Their most consistent finding was that all species tended to avoid "dense grass" habitats (i.e., primarily sawgrass). Otherwise, the evidence suggested a tendency for most species to prefer more open, heterogeneous mixes of emergent wet-prairie and slough vegetation. Such patches were often embedded in a matrix of tree islands, and typically were associated with transitional hydrologic conditions.

Dense, tall vegetation probably physically impedes a bird's movement and may also reduce a bird's or a flock's ability to remain vigilant against predators and disturbances. That the latter may be important became evident during my attempts to approach feeding flocks on an idling airboat for the purpose of conducting

observations. The experience suggested that individuals and groups of birds--particularly ibises--flushed more quickly from foraging positions within taller vegetation that restricted their view of the boat than when they were in more open areas. One might also speculate that the densest cattail and sawgrass habitats might harbor reduced prey populations; however, throw-trap sampling in dense sawgrass at Loxahatchee National Wildlife Refuge revealed relatively high densities of small fish, primarily Gambusia holbrooki (C. F. Jordan pers. comm.). It therefore seems most likely that physical constraints render these habitats less attractive to foraging birds.

Use of submerged vegetation and open-water habitats, and the lake as a regional drought refuge. When surface-water levels dropped sufficiently to expose beds of submerged vegetation, all species took advantage of the new foraging habitat. Perhaps the strong selection of these habitats indicated for all species was a matter of default, since most of the upper marshes were dry. Moreover, the large influx of birds at this time probably in part reflected the fact that foraging conditions in the Everglades and other surrounding wetlands were poor due to the drought (P. C. Frederick and G. T. Bancroft pers. comm.). However, prey sampling confirmed that these habitats, especially thick beds of Hydrilla and Vallisneria, contained very dense concentrations of small fishes and grass shrimp (McIvor and Smith 1992; Chick and McIvor 1994). Observations also revealed relatively high foraging success and caloric intake rates (McIvor and Smith 1992). It was not possible to determine to what degree the high densities of prey were the result of drought-related concentration effects. Regardless, these habitats did represent a rich food source for wading birds.

The data for the less common Wood Storks and Roseate Spoonbills provided the strongest evidence that an unusual number and variety of wading birds were drawn to the lake during the drought periods. Roseate Spoonbills generally remain in coastal

habitats, but small numbers of dispersing young frequently visit the Lake Okeechobee region (Palmer 1962; and see Zaffke 1984). However, during the drought in both 1989 and 1990, an unusually large group of up to 75 immature birds remained at the lake for up to 10 weeks. Smaller groups foraged with mixed feeding flocks typically in open flats between mats of submerged vegetation, but the entire group established a primary loafing and roosting area along the banks of one canal.

Wood Storks have nested in small numbers around the lake (Zaffke 1984; David 1994a) and are regularly seen foraging in the area. However, the data gathered in this study and by Zaffke (1984) indicate that Wood Storks are attracted to the lake in large numbers only when the stage is dropping and below 4.6 m (nearer to 4.3 m in most cases). Both studies indicated that the largest numbers occur during severe drought periods (1981 during Zaffke's study and in 1990 during this study, with lake stages below 3.0 and to 3.2 m, respectively). The large flocks of Wood Storks seen during this study typically included both immature and adult birds. This suggests that the lake was a more universally important resource for Wood Storks than for Roseate Spoonbills (also see Browder 1976). The winter-spring recession of 1991/92 did not attract storks to the lake, probably because water levels did not recede sufficiently. However, differences in long term antecedent hydrologic conditions may have influenced the trend (sensu Frederick 1993). The 1992 recession followed a two and a half-year drought cycle, whereas the 1989 recession followed a three-year period of relatively high water. The abundance of medium to large sunfishes--a frequent target of foraging Wood Storks on the lake (unpubl. data)--probably increases with prolonged flooding (Loftus et al. 1990). The increase in productivity would then lead to richer, more attractive concentrations as surface-water levels receded.

All species took advantage of prey resources available within and around exposed beds of submerged vegetation during the drought. However, Snowy Egrets appeared to profit from submerged vegetation and floating-mat habitats even during non-drought periods. The species' use of aerial foraging techniques--often involving small, floating water hyacinth islands as launching platforms--was the key to its successful use of the habitat (also see Edelson and Collopy 1990). This tendency for Snowy Egrets to use more open habitats was also documented by Murdich (1978), who studied several species in a large prairie-wetland ecosystem in Alachua County, Florida. He found that Snowy Egrets, more often than Great Blue Herons, Tricolored Herons and Great Egrets, foraged mostly in open drainage canals and pools, flooded diked areas, and other areas of relatively low vegetation density. Similarly, Jenni (1969) studied several species around a small lake on the University of Florida campus in Gainesville, and commented that Snowy Egret's tended to feed "in open areas and along edges of openings." Kent (1986a) found that Snowy Egrets foraged least efficiently in comparison to Tricolored and Little Blue herons (Snowy Egrets estimated to require an average daily foraging period two times longer). Snowy Egrets may therefore experience greater pressure to reduce their foraging-niche overlap with other species.

In this study, Great Blue Herons showed a strong tendency to forage in open habitats, including open flats at low lake stages--sunfish bedding areas--and open edges along canals and on the rocky east-side at a variety of lake stages. Evidence gathered under nests and during observations of feeding flocks confirmed that Great Blue Herons often consumed small bass and large sunfish, shad and shiners, types of prey rarely captured by other species (unpubl. data). Otherwise, it is not surprising that most species underutilized the most open, outer fringe habitats. Open-water areas are

less frequently populated by the smaller fishes and invertebrates that most wading birds appear to prefer (Werner et al. 1977), and there are no physical barriers in open water to restrict fleeing prey, potentially making it more difficult for wading birds to secure available prey. At the height of the drought, most species (Great Egrets, White Ibises, Snowy Egrets, and Wood Storks, in particular) occasionally foraged in open or sparsely vegetated outer fringe habitats, but except for Great Blue Herons, always only in large flocks. The presence of large flocks appeared to elicit chaotic movements among the fishes in the midst of the group, and this provided at least temporarily profitable foraging opportunities (pers. observ.).

Jenni (1969) noted that Tricolored Herons also tended to forage along the edges of canals and steep banks, and from floating or submerged vegetation in deeper water. This study indicated that Snowy Egrets were more likely to forage in submerged and mat vegetation habitats, but following the drought, Tricolored Herons continued to select SUB habitats longer into the 1991 season than Little Blue Herons and Great Egrets. Furthermore, although the selection analyses did not adequately reflect such details, solitary Tricolored Herons--like Snowy Egrets--often used floating lotus leaves to gain access to prey-rich Hydrilla beds. Murdich (1978) found that Tricolored Herons were the most generalized in their use of habitats in comparison to Snowy Egrets, Great Egrets, and Great Blue Herons. According to the results of this study, this was not the general rule at Lake Okeechobee; however, aerial surveys of both Tricolored and Little Blue herons were biased towards those occurring in mixed flocks. Both species, but particularly Tricolored Herons, often foraged alone in a wider variety of habitats, but went undetected on aerial surveys. As noted by Jenni (1969) as well, I often observed solitary Tricolored Herons foraging along the edges of canals.

Great Egrets, like Snowy Egrets, periodically used aerial foraging techniques to access deep open-water habitats dominated by primarily Potamogeton and Hydrilla. However, unlike Snowy Egrets, Great Egrets appeared to require the help of persistent winds for lift and support. The 1990 spring season featured such winds, and a small number of birds that nested in the center of Fisheating Bay appeared to profit from aerial foraging. They fed their nestlings an unusually rich collection of larger fishes, and their nesting success and productivity were among the highest for the study (Collopy and Smith 1991). Edelson and Collopy (1990) found that most common Florida wading bird species would use aerial techniques when presented with a rich enough source of prey. In that case, such conditions were present at a hyper-eutrophic lake where large schools of fish often gathered at the surface. Birds were able to take advantage of numerous launching points, including elevated woody perches around the perimeter and fish-net floats strung across the lake.

Management Implications

Management of exotic and nuisance vegetation. The control of exotic and nuisance vegetation is a major management issue in Florida, and several species are of concern at Lake Okeechobee. The first is Melaleuca (see Bodle et al. [1994] for a general discussion); according to this study, wading birds do not use the trees for nesting and do not forage within typically dense stands of the species. The further expansion of Melaleuca following the drought and fire cycle only served to eliminate productive Eleocharis and Rhynchospora flats that previously occurred at the margins of the Melaleuca forests along the western margin of the lake. The fact that Melaleuca was able to expand its range following the drought was one of the few apparent disadvantages of the drought.

The second species of concern is cattail, a native species but one that has expanded its coverage and dominance in many areas in response to the addition of nutrient-laden agricultural runoff and unnatural manipulation of hydrologic regimes (Davis 1989). Again, this study suggests that foraging and nesting wading birds do not benefit from dense stands of cattail. Unlike for Melaleuca, however, the drought/fire cycle at least temporarily controlled the spread of cattail in many areas, and this provided the opportunity for productive stands of Polygonum to develop and persist until the lake stage returned to high levels.

Another exotic species of concern is Panicum repens, which typically dominates the northwestern Indian Prairie region. This study indicated that wading birds, particularly Great Egrets, frequently foraged in this area at higher lake stages (also see Zaffke 1984). My observations suggested that when water levels in the Panicum repens flats remained low for extended periods, thick, continuous-cover mats of dead wrack and live plants formed. At this point, other species of vegetation were excluded, access to the underlying surface water was restricted, and wading birds foraged in other habitats. The fires that burned through the Indian Prairie area in 1990 and 1991 removed the excess wrack, and regeneration after reflooding led to comparatively sparse stands that attracted foraging wading birds. Similarly, conditions in late 1988 and early 1989 suggested that extended periods of high water also produce sparser stands of Panicum, and therefore result in attractive foraging habitat for wading birds once water levels decline to suitable depths. Thus, periodic low-water/fire cycles or extended periods of high water may be necessary to ensure the suitability of Panicum repens habitats for foraging wading birds.

The more controversial issues concern management strategies to deal with Hydrilla and water hyacinth. Currently, the SFWMD oversees an extensive program of

herbicide spraying to control the spread of water hyacinth, Hydrilla, and water lettuce, particularly in waterways and bays frequented by boaters and fishers (Langeland and Joyce 1987). Sampling has indicated that thick beds of Hydrilla on the lake support very high densities of small fishes and grass shrimp (McIvor and Smith 1992; Chick and McIvor 1994). Moreover, when they are accessible, these habitats attract large numbers of foraging wading birds. Although other native submerged species such as Vallisneria also harbored large populations of small fish (McIvor and Smith 1992) and should probably be emphasized more in management plans, one cannot ignore the benefits of Hydrilla in this regard. Moreover, only Hydrilla forms the thick, topped-out mats that allowed wading birds access to otherwise inaccessible deep-water habitats. Of course, it is exactly this feature that annoys boaters trying to access their favorite fishing holes, and excessively thick and extensive beds may hinder the growth and development of large game-fish species (Colle and Shireman 1980).

In the case of water hyacinth, my observations suggested that wading birds rarely forage within healthy mats, but often use smaller clumps for support while foraging at the edges and launching aerial attacks over the adjacent submerged beds (also see Murdich 1978). My observations also indicated that several species, particularly Snowy Egrets, flocked to large, recently-herbicided mats of water hyacinth. Such sites typically supported activity for only a few hours or less, and birds were first attracted within hours of the herbicide spraying. One might speculate that the food obtained at this time was not entirely safe for consumption given the recent application of herbicides and the tendency for wading birds to consume quantities of vegetation--particularly abundant Lemna--with their target prey (unpubl. data). Nonetheless, observations of foraging birds confirmed typically high capture rates and at least moderately high caloric intake rates (unpubl. data). Thus, extensive mats of healthy

water hyacinth do not appear to benefit wading birds. However, the presence of smaller mat-islands provides access to otherwise inaccessible open-water and submerged vegetation habitats, and the relationship between herbicided mats and wading bird foraging is an intriguing one that demands further study.

Hydrologic and related concerns. The results of this study suggest that to attract large populations of foraging wading birds to the lake, two primary criteria must be met: 1) lake stages should be managed to remain at or below about 4.6 m to insure the availability of some foraging habitat; 2) management schedules should encourage a steady, moderate-paced spring recession that coincides with the normal Florida dry season and usual wading bird nesting season (i.e., January - June). The ideal magnitude for a spring recession is less certain. Evidence collected during this study suggested that the most productive foraging conditions occurred when the recession was sufficient to expose beds of submerged vegetation to foraging birds (i.e., lake stages below about 3.7 m). David (1994b) found that, during the 12 years prior to this study, combined-species foraging populations usually increased in response to dropping lake stages if the drying rate exceeded -0.15 m per 60 days. In this study, the largest foraging populations were attracted during 1989 and 1990 at the height of the drought, with 60-day antecedent drying rates of up to -0.51 m in June 1989 and -0.42 m in May 1990. However, the lake stage declined at a maximum rate of -0.31 m over the 60-days prior to the end of May 1992, but foraging populations did not increase much because the lake stage dropped below 4.6 m for only a short time. Moreover, most species temporarily emigrated from the lake during reversals in the 1989 drying trend, despite higher overall recession rates than in 1990. This suggests that the steadiness of the recessions may be more important than the rate or magnitude of decline. Further support for this contention was provided by the logistic regression

analyses of nest failure summarized in Chapter 5; the surface-water trend variable "days-of-rising-water" consistently exerted more influence in the regression models than “drying-rate” variables.

Most species achieved the highest per nest productivity at the height of the drought in 1990 (Chapter 4). Snowy Egrets, Tricolored Herons, and White Ibises also initiated the most nests 1990. However, both Great Blue Herons and Great Egrets initiated more nests in 1989 and 1992 than in 1990 or 1991. Moreover, nest productivity in 1989 among the latter species was only slightly lower than in 1990, and Great Blue Herons also achieved comparable production levels in 1992. This suggested that the combination of high winter water levels and an early spring recession was the scenario that most attracted these species for nesting.

Little Blue Herons were also unusual in showing a steady decline in nest numbers through the study, with the highest effort and productivity in 1989 (Chapter 4). The fact that Little Blue Herons did not initiate more nests again in 1992 with the return of deeper water, suggests that long-term antecedent hydrologic conditions may have been the key to their response. During this study, Little Blue Herons relied more heavily than other species on grass shrimp for feeding their young (McIvor and Smith 1992), as has been demonstrated elsewhere (e.g., Rodgers 1982). Loftus et al. (1990) and Loftus and Eklund (1994) determined that short-hydroperiod marshes in the Everglades support depauperate populations of most aquatic organisms compared to nearby longer-hydroperiod marshes. One of the most dramatic differences was shown for grass shrimp (Loftus et al. 1990). Thus, extended periods of high or at least moderate depth water may be essential for a subsequent recession to produce advantages for nesting Little Blue Herons.

Hydrologic conditions also play a critical role in determining suitable locations for nesting colonies. At the height of the drought most interior colonies were abandoned in preference for island colonies still surrounded by water (Chapter 4). Two reasons for the shift may have applied: 1) the nesting birds may have relocated closer to favorable submerged-bed foraging grounds; 2) the move to flooded islands may have precluded invasions by terrestrial nest predators. Regardless, all species used a wider variety of colony sites in 1989 and especially 1992 than in 1991 and especially 1990. Consequently, striving for maintenance of moderate lake stages (e.g., 3.7-4.3 m) rather than lower lake stages may provide more diverse opportunities for both nesting and foraging, and may ultimately ensure a more flexible and resilient system.

There is also the issue of the relatively consistent bimodal distribution of numbers of ibises each year. The trend suggested that some birds attracted to the lake to feed early and late in the year went elsewhere to nest, which in turn suggests that nesting opportunities at the lake were in some way limited. David (1994a) documented a long term decline in nest numbers at the lake over the period 1977-1988, with White Ibis a prominent example. He attributed the decline to the negative influence of higher stage-regulation schedules on the availability of foraging conditions and on the health of willows. A decline in the health of willows--the primary nest substrate--might have been partly responsible for the abandonment of the King's Bar nesting colony, which historically was the most consistently occupied and largest colony on the lake. Perhaps the ibises in particular have not found other locally available sites as appealing.

The best active management strategy will likely involve cycles of manipulation, with planning based on a multi-year window approach rather than a static annual-pattern approach. The typical annual pattern might include a fall-winter peak of 4.6-4.9 m drawn down 0.3-1.0 m from January through June. However, once every several

years the lake stage might be kept lower through the winter and allowed to drop to the 3.0-3.6 m range during the dry season to expose prey-rich submerged beds, invigorate essential willow stands, and allow fires to burn away cattail and Panicum wrack, recycle nutrients, and encourage the establishment of attractive successional vegetation complexes. Similarly, periodically encouraging multi-year periods of higher stages might enhance the productivity of fish and macro-invertebrate populations. Placing a general emphasis on maintaining long-hydroperiod marshes (but not necessarily deep water) may also be a good strategy with respect to managing for the endangered Snail Kite. Kites apparently prosper when upper-elevation Eleocharis flats remain flooded year round, because this insures healthy populations of their primary prey, apple snails (Pomacea paludosa; Bennetts et al. 1994). Moroever, at lower lake stages the kites often nest in relatively unstable cattail and Phragmites toward the outer margins of the littoral zone, rather than in trees at the periphery of the lake. There nest success when cattail or phragmites is the nest substrate tends to be low because many nests collapse for lack of proper support (Bennetts et al. 1994). Because both high and low lake stages encourage ecosystem elements favorable to wading birds, the wisest and least costly management strategy probably will be one of benign neglect; i.e., allow natural hydrologic fluctuations to run their course and institute significant control measures only to avoid environmental or economic disaster.

A final critical point is that the Lake Okeechobee ecosystem must not be studied or managed as an isolated system, particularly not where wading birds are concerned. Wading birds are highly mobile species, and what happens at Lake Okeechobee is always at least in part related to the quality of conditions in the Everglades and other southern Florida wetlands, if not to conditions throughout the southeastern United States. Again, the occurrence of so many birds on the lake in mid-1989 and mid-1990

might have had as much to do with foraging conditions being poor in the Everglades and in other regions as it did with conditions being favorable at the lake. Moreover, conditions at the lake need not be ideal for wading birds every year, as long as regional management plans help insure the availability of suitable foraging and nesting habitat somewhere in the southern Florida region. Accordingly, a regional management perspective is essential.

CHAPTER 3
FORAGING FLIGHT DYNAMICS AND PATTERNS OF HABITAT USE WITH RELATION TO NEST PRODUCTIVITY, AND FORAGING SOCIABILITY AMONG FOUR NESTING SPECIES

Introduction

For most species of birds, the energetic and logistic demands of nesting peak when chicks hatch and adults are challenged with the task of supplying food to their rapidly growing chicks (e.g., Kahl 1964; Kushlan 1981). The added strain may be particularly great for species with nidicolous (nest-bound) young, because the adults must operate as "central-place foragers" (sensu Orians and Pearson 1979) and make repeated trips to and from the nest each day. If food is plentiful near the nest, then the added energetic burden may not be great, but it will increase as the distance to profitable foraging grounds increases. If the distance is too great, adult birds might choose to abandon their nesting effort because the energetic cost of travel exceeds the benefits of high quality foraging habitats (Wittenberger and Hunt 1985; Bryan and Coulter 1987). Studies of ciconiiform wading birds in the Florida Everglades have indicated a positive correlation between colony abandonments and foraging-flight distances (Frederick and Collopy 1988; Bancroft et al. 1990, 1994). However, Frederick and Spalding (1994) later suggested, based on energetic calculations, that the abandonments probably occurred because increasing flight distances reduced the rate and total amount of prey delivery to nestlings, not because the adults were physically taxed. Regardless, any study of the causes of reproductive failure among

wading birds should consider how variation in both the quality and cost of travel to foraging habitats affects the species studied (Bancroft et al. 1994; Frederick and Spalding 1994; Ogden 1994).

As part of a 4.5-year study of wading bird nesting and foraging ecology at Lake Okeechobee, Florida (see Fig. 3-1 for a geographic overview of the region), I documented foraging-flight characteristics for 960 individuals of four species of commonly nesting wading birds at times when nestlings were being fed. The study species were Great Egrets, Snowy Egrets, Tricolored Herons, and White Ibises. In this chapter, I summarize my findings on flight times and distances, and compare these statistics with estimates of nest success and nestling production (see Chapter 4 for a detailed treatment of nesting ecology). The research hypothesis was that, if the energetic demands of repeated foraging flights are an important constraint, then increasing flight times and distances should translate to decreasing nest success and productivity.

I also analyze the foraging flight dynamics and habitat choices of nesting adults in relation to hydrologic trends. Managing lake water levels is a primary concern for resource managers in the region (Aumen 1994). The lake serves as a regional flood control and water supply facility, supports a multi-million dollar commercial and sport fishing industry, and is an important resource for many species of both game and non-game wildlife (Aumen 1994). The demands of these interests often conflict, and so developing balanced approaches to management is a subject of considerable debate. Wading birds are considered bioindicators of change in hydrological and ecological conditions in wetland ecosystems (e.g., Custer and Osborn 1977; Curry-Lindahl 1978; Hafner and Britton 1983; Bildstein et al. 1990; Kushlan 1986b, 1993; Ogden 1994), and therefore understanding how wading birds respond to fluctuating hydrologic conditions

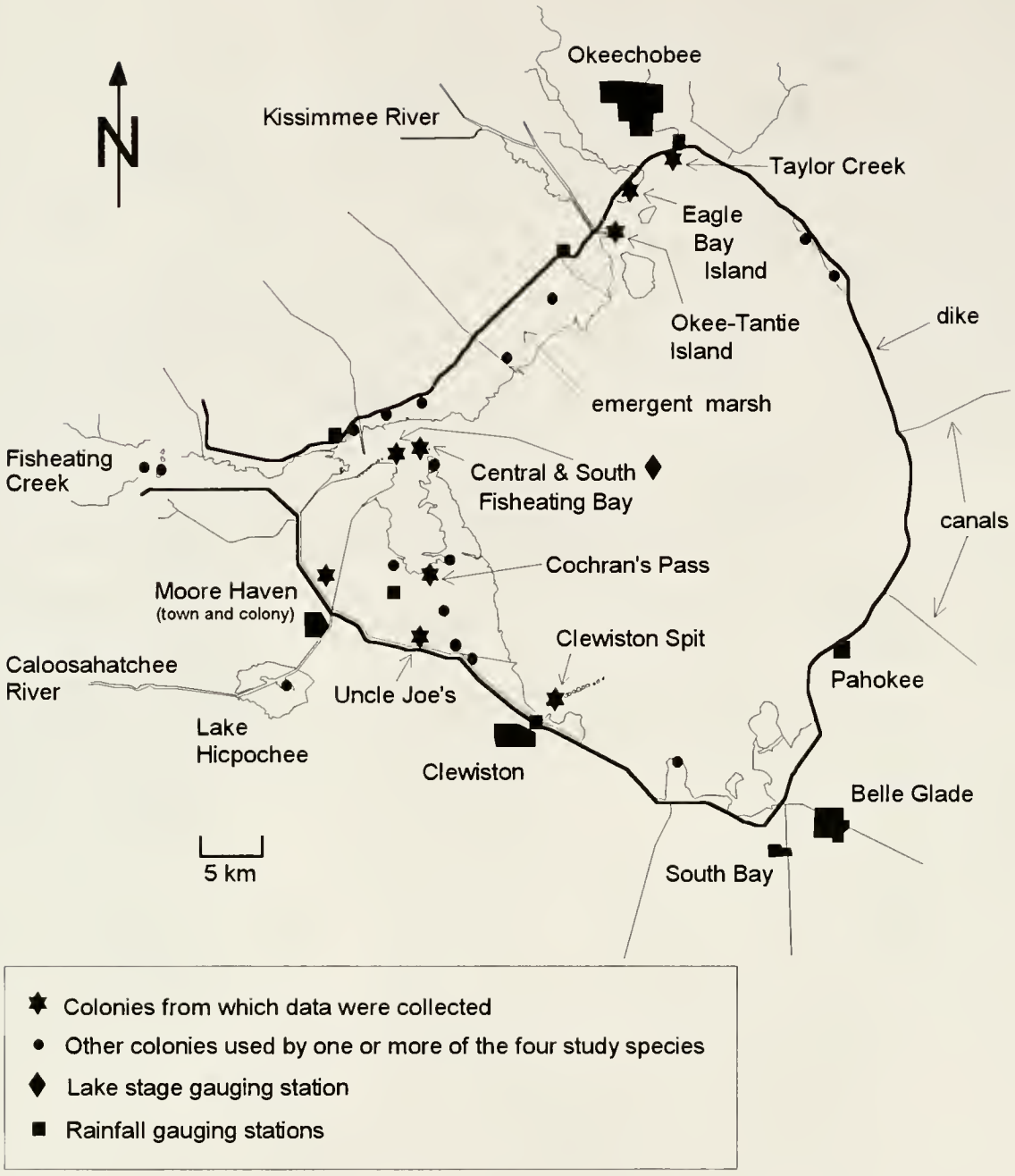


Figure 3-1. A geographic overview of the Lake Okeechobee area showing the locations of nesting colonies used by the four study species, and showing the locations of lake stage and rainfall gauging stations.

is often a focus of management concerns. Hydrologic trends determine water depths and influence both the distribution of vegetation (Richardson and Harris 1994) and the productivity of prey populations (Loftus et al. 1994), and therefore are a primary determinant of wading bird foraging efficiency and consequently nesting success (Bancroft et al. 1994; Frederick and Spalding 1994; Ogden 1994). The 1989-1992 study period spanned a two-year drought (Fig. 3-2) that resulted in a 10-year record low lake stage in May-June 1990 (3.2 m NGVD; NGVD = National Geodetic Vertical Datum of 1929, essentially equivalent to height above mean sea level; for convenience, I will henceforth omit the NGVD qualifier). An unusually high estimated total of over 50,000 foraging wading birds congregated on the lake at this time (Chapter 2). Most nesting species also achieved the highest reproductive success for the study in 1990 (Chapter 4). The probability of nest failure was generally lowest when surface-water levels were declining steadily and the mean lake stage was low to moderate (3.5-4.1 m; Chapter 5). Studying foraging-flight dynamics added another dimension to the picture and highlighted unique aspects of the foraging ecology of nesting adults. In particular, the study enabled a determination of whether or not the pronounced hydrologic fluctuations contributed to shifts in foraging habitat use and changes in foraging flight distances that might have affected the energetics of nesting.

Lake Okeechobee is nearly surrounded by a large earthen dike (Fig. 3-1). Thus, there is an abrupt transition from extensive emergent marsh (400 km^2), submerged vegetation, and open-water habitats inside the dike to a wide variety of natural and artificial wetland habitats outside the dike. The latter include: the Kissimmee River and Fisheating Creek floodplains (see Fig. 3-1); diverse pocket and slough wetlands interspersed with cattle pastures to the north and west; myriad agricultural field ditches and canals to the south and east; and residential canals and

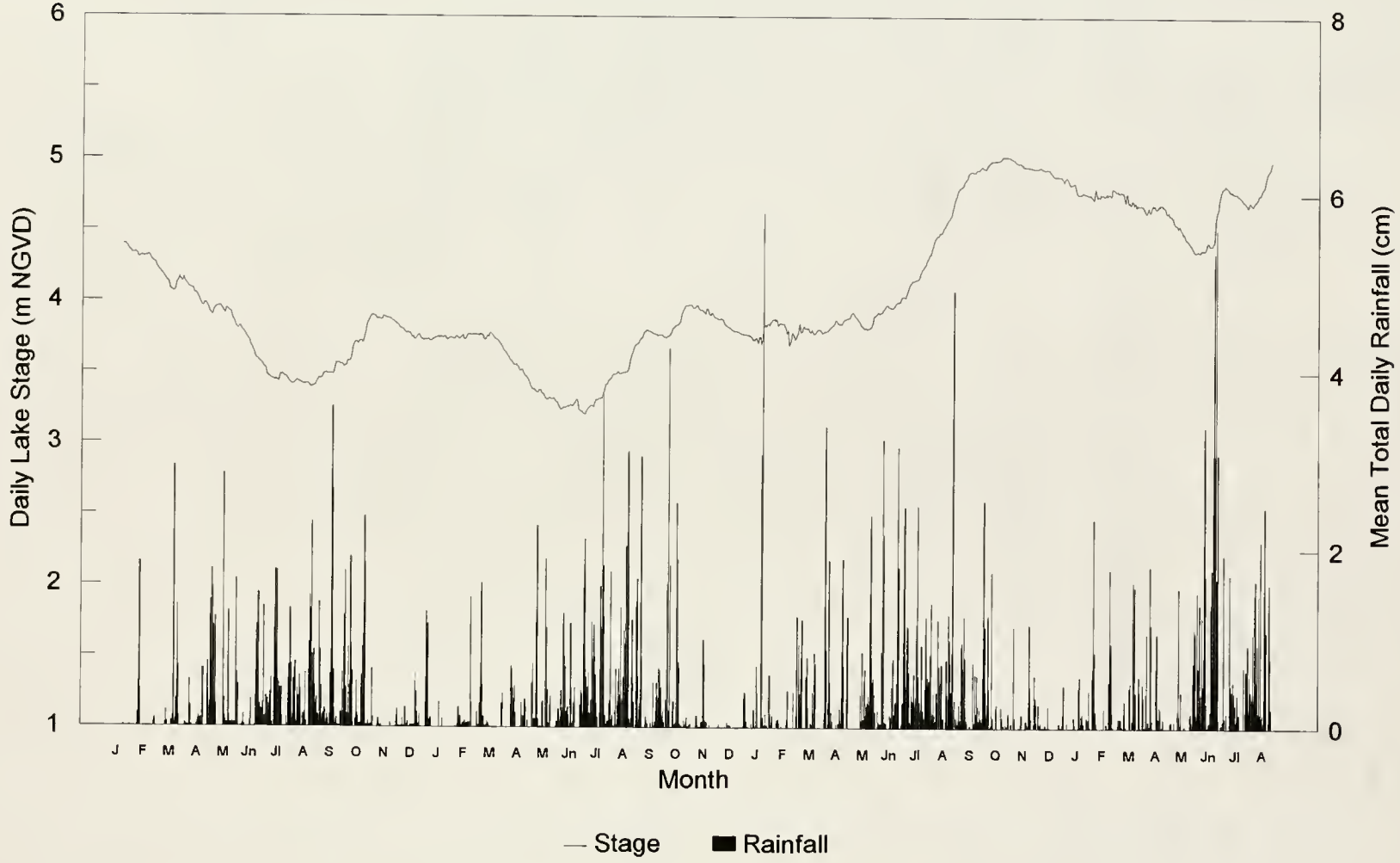

Daily Lake Stage (m NGVD)
Mean Total Daily Rainfall (cm)
6
5
4
3
2
1
8
6
4
2
0
J F M A M Jn Jl A S O N D J F M A M Jn Jl A S O N D J F M A M Jn Jl A S O N D J F M A M Jn Jl A
Month
Stage
Rainfall

Figure 3-2. Daily lake stage and basin-average total daily rainfall from January 1989 through August 1992.

retention ponds in several areas. The lake region thus provides wading birds with an unusually diverse array of foraging opportunities within a relatively limited area. A previous study indicated that wading bird use of off-lake habitats such as the Fisheating Creek watershed increased at high lake stages (Zaffke 1984). Wading birds are generally vagile species that readily disperse in search of suitable foraging and nesting habitat (Kushlan 1976c, 1978a, 1981, 1986b; Browder 1976; Byrd 1978; Bancroft et al. 1994; Ogden 1994), and although the dike around Lake Okeechobee creates a stark habitat boundary, it certainly does not limit the movement of wading birds. Understanding how hydrologic trends influence the on- and off-lake foraging habitat choices of birds that nest on the lake, and elucidating the relative importance of off-lake habitats for nesting birds will help in devising a management plan that explicitly recognizes the vagile nature of wading birds. High lake stages (>4.3 m) eliminate foraging habitat on the lake (Chapter 2), but moderately high stages increase the availability of suitable nesting habitat compared to low stages (Chapter 4). Thus, management plans that encompass off-lake wetland habitats may insure that the lake is a resource for nesting wading birds even when foraging conditions on the lake are suboptimal.

Lake management issues were the driving force behind my work, but through my studies of foraging-flight dynamics I also gained insight into the social aspects of wading bird foraging. Considerable debate has focused on the issue of whether or not species benefit from colonial nesting because individual pairs can exploit conspecifics or similar species for information about profitable foraging locations (Ward and Zahavi 1973; Krebs 1974; Custer and Osborn 1978; Pratt 1980; Erwin 1983; Waltz 1983). As part of my study, I documented species-specific tendencies for traveling in groups and for joining other foraging birds at chosen feeding sites. I discuss whether species

differences in degree of sociability reflect differences in foraging behavior, and discuss the implications concerning the relative importance of local enhancement (sensu Evans 1982) and information exchange at the colonies (sensu Ward and Zahavi 1973).

Study Area and Methods

Study Area

Lake Okeechobee is the third largest freshwater lake in the United States (1,732 km^2 surface area; Herdendorf 1982). The average water depth in the lake is 2.7 m. The lake drains a watershed of nearly 12,000 km^2, primarily through the Kissimmee River from the northwest (Fig. 3-1), and is situated upstream of the remnant Everglades and Florida Bay. The South Florida Water Management District (SFWMD) and the US Army Corps of Engineers have primary responsibility for management of the lake stage. Most surface-water inflows and outflows are controlled by the dike and through canals by hurricane gates, locks, and pumping stations. However, although human regulation affects the lake stage to a degree, mostly at high stages, the primary factor controlling water levels in the lake is regional rainfall (Aumen 1994). The lake serves as a flood-control, water-storage, and recreational facility serving the needs of an extensive agricultural industry and a burgeoning urban population. The lake also supports a multi-million dollar commercial and sport fishing industry. Management of the lake and its resources garners considerable attention, because the demands of these diverse interests often conflict. Aumen (1994) provides a more detailed account of the natural and management history of the lake. Chapters 2 and 5 provide detailed accounts of the hydrologic and climatic conditions that prevailed during the study, and therein I discuss how variation in environmental conditions influenced the nesting and foraging

ecology of wading birds. Chapter 4 provides a detailed history of nesting during the study, and David (1994a) discusses the history of nesting during the twelve years prior to the study. Detailed maps of vegetation communities on the lake can be found in Chapter 2 and in Richardson and Harris (1994).

Field Methods

Each year from 1989-1992, I followed individual and small groups of unmarked, nesting adult birds from colonies to foraging grounds in a Cessna 172 fixed-wing aircraft. Each season, I began following birds once eggs began to hatch and continued flights until most nestlings had fledged. I concentrated on large, mixed-species colonies located on the lake in which I conducted concurrent nest success studies (Chapter 4). I also periodically followed birds from other colonies. I conducted following flights every week. Each week I tried to follow some individuals of each species from each of the focal colonies. I conducted surveys throughout the day, as long as activity levels were sufficient to insure a consistent source of birds to follow.

I began each following-flight by circling above the chosen colony at an altitude greater than 150 m, and randomly chose a bird or closely associated, conspecific group of birds to follow. I then monitored the progress of the bird(s) by flying in slow, wide circles around and above the bird(s) at horizontal and vertical distances of no less than 150 m. I followed each bird until it landed in an area where foraging was possible and remained in the same spot during the time it took to record a LORAN C coordinate (accurate to 0.18 km), a stop time, a description of the chosen habitat and flock joined, and a photograph of the area. Recording these data usually took 2-3 minutes. If the bird began moving again during this time range, I continued the flight. The only time I deviated from this protocol was when I had followed a group of birds that did not all

land in the same location. In this case, I attempted to document the first landing spot for all birds, but was unable to record the final details for each until the last bird had landed and I could then return to previous landing spots to record additional data. Sometimes I was forced to abandon individuals that ultimately followed widely divergent paths. In these cases, I continued to follow the larger of the split groups or randomly chose one of a split pair to finish following. I recorded the total flight time--including any temporary stops--in seconds, and eventually calculated the straight-line travel distance in kilometers based on LORAN coordinates for the colony and the landing point.

Analytical Methods

A primary assumption behind most parametric statistical tests is that the observations to be analyzed are independent of one another; i.e., the value of--or random error associated with--a given observation is not related to other such values in any systematic way (e.g., see Sokal and Rohlf 1981: 401-402). Some of the birds I followed flew in groups from the colony to foraging sites. The foraging habitat choices of each bird in such groups may have depended on the results of social interaction. If so, each set of individual-bird observations would be interdependent, and the data should be analyzed as if it were a single observation. However, it is also possible that some groups formed simply because several birds happened to depart for a known foraging location at the same time. Thus, eliminating all apparently redundant group observations may unnecessarily sacrifice valid data. Accordingly, to determine the effect on results, where appropriate I ran the analyses discussed below twice, once with all individual-bird observations included, and once with each set of group observations considered as a single observation. In all such cases, I found that although there were subtle differences in significance levels, there were no marked

differences in the conclusions suggested. Therefore, all the results presented below were derived from datasets that included individual-bird observations as independent units.

Flight distances and patterns of habitat use. I used a standard least squares analysis of variance (ANOVA) with Bonferroni *t*-test multiple comparisons (performed in SYSTAT, Wilkinson 1990) to elucidate annual differences in log-transformed (ln[x]) lakewide mean flight distances for each species. I used a likelihood ratio chi-square (χ^2) test of independence (Sokal and Rohlf 1981: 735-738; performed in SAS, SAS Institute Inc. 1988) and χ^2 multiple comparisons described in Fleiss (1981: 141) to asses whether the proportion of on- and off-lake flights varied from year to year.

I conducted multiple regression analyses for each species to determine whether foraging flight distances were influenced by a series of hydrologic variables. The independent variables included: the mean lake stage on the day of each flight; the number of days of rising water (intermittent and continuous) during the 30-days prior to each flight; and the total rainfall during the 30-days prior to each flight. I acquired daily lake stage (an index to but not equivalent to water depth) and rainfall records from the SFWMD. The stage readings were collected at a central, open-water gauging station (Fig. 3-1), and I assumed these data represented basin-average conditions (see Chapter 2 for a discussion of potential limitations). Rainfall was measured at several, primarily perimeter gauging stations (Fig. 3-1), and I matched data sources to colonies based on proximity (mean distance 4.3 km, maximum 7.3 km). I calculated the days-of-rising-water variable from the stage data to reflect patterns of fluctuation in surface-water levels. I log-transformed (ln[x]) the flight distance data to normalize residuals. For this analysis, I pooled data from all years and colonies to maximize sample sizes

and the environmental variability reflected in the analyses. I began by calculating saturated models that included all possible interactions, but ultimately eliminated interaction variables not significant at the $P = 0.05$ level (using the backward selection method in SYSTAT; Wilkinson 1990).

I conducted likelihood ratio χ^2 tests of independence to elucidate relationships between patterns of habitat use and lake stage ranges. I aggregated the foraging-flight observations according to end-point habitat types and the current lake stage. To insure reasonable sample sizes, the habitat categories to which I assigned observations represented only broad-scale vegetation/habitat types, and the categories varied some from species to species. The number of lake stage categories and the cutoff points for each also varied some depending on the distribution of data for each species. I distinguished three classes of off-lake habitat: 1) AG - agricultural field--primarily sugar cane--ditches and canals and occasionally flooded fields, located just north of Moore Haven and around the south end of the lake (Fig. 3-1); 2) PS - cattle-pasture ditches and ponds and occasionally flooded pastures interspersed with remnant pocket wetlands and natural hardwood-hammock and pine-woodland slough wetlands, located west and north of the lake; and 3) PANH - residential fish-cleaning stations and associated canals, and bait shops where Great Egrets panhandled fish scraps from fishers, located around the towns of Okeechobee and Clewiston (Fig. 3-1). The on-lake habitat categories included: 1) MS-OF - mixed submerged vegetation--primarily Hydrilla, Vallisneria, and Potamogeton--and outer littoral-zone fringe habitats that included emergent stands of Scirpus, cattail, lotus, and Panicum hemitomon, and frequently floating mats of water hyacinth and duckweed; 2) MS-A - the same as MS-OF, but usually deeper habitats that Snowy Egrets and Great Egrets accessed by aerial

foraging; 3) HM-LOT - mixed Hydrilla mat and lotus habitats, a subcategory of MS-OF that Snowy Egrets and Tricolored Herons were particularly attracted to; 4) HM-HYC - mixed Hydrilla and hyacinth mats, another subcategory of MS-OF distinguished in the Tricolored Heron analysis; 5) MP, mixed emergent wet-prairie usually dominated by mixes of Eleocharis, Rhynchospora, Panicum, Nymphaea, and cattail; 6) MTR, "middle"-littoral-zone transitional bog and slough habitats featuring Pontedaria and diverse emergent/submergent mixes; and 7) UTR, shallow, upper-littoral-zone transitional habitats featuring grass/sedge mixes, Polygonum, and flooded terrestrial species.

Because the lake is surrounded by an earthen dike, lake stage fluctuations do not directly influence the hydrology of habitats outside the dike. However, lake stage readings provide a general index to surface-water conditions in the region, in that fluctuations in the lake stage are due primarily to variation in regional rainfall (Aumen 1994). In other words, when water levels are high and rising on the lake they tend to be high and rising adjacent to the lake. Therefore, for purposes of the above analyses, I assumed that the lake stage variables reflected average hydrologic conditions both on and off the lake. In addition, the rainfall data were collected at primarily perimeter gauging stations, and therefore applied equally well to habitats on and off the lake.

Foraging sociability. I conducted a likelihood ratio χ^2 test of independence with χ^2 multiple comparisons to elucidate whether species differed in their tendency to travel alone or in groups from colonies to foraging sites. I used a standard least squares ANOVA with Bonferroni *t*-test multiple comparisons to determine whether species differed with regards to the size of the groups they traveled in when they traveled in groups (log-transformed group size data).

I conducted a likelihood ratio χ^2 test of independence to determine whether species differed in their tendencies to land alone, near others, or in the immediate vicinity of other birds at foraging sites. A bird that landed alone landed in a habitat patch entirely devoid of other birds; i.e., the presence of other birds could not have affected the birds choice of the particular foraging spot. A bird that landed near others landed in a habitat patch where one or more other birds were already foraging, but did not join a concentrated feeding flock. Estimating distances from the air is difficult, so the definition of what qualified as near was imprecise. Essentially, if a bird landed such that its foraging movements would intersect those of other birds, then I classified it as having landed in the immediate vicinity of others. Otherwise, if the bird chose a foraging location where its choice may have been influenced by the fact that other birds were foraging nearby in the same habitat, but the distance between the bird and others was such that it was unlikely the bird would directly interact with others, then I classified it as having landed only near others.

I conducted a separate likelihood ratio χ^2 test of independence with χ^2 multiple comparisons to determine whether species differed in their tendency to join conspecifics at foraging sites. I limited the data to followed birds that landed near or in the immediate vicinity of others. I also conducted a standard least squares ANOVA with Bonferroni *t*-test multiple comparisons to determine whether species differed with regards to the size of the feeding flocks each joined. Again, I limited the data to followed birds that landed near or in the immediate vicinity of others. I calculated flock sizes as the total of all birds considered near or in the immediate vicinity of the followed bird. I log-transformed the flock size data to normalize residuals.

Results

Foraging-Flight Dynamics and Patterns of Habitat Use

Great Egrets. I followed 356 Great Egrets from five colony sites over the four-year study period. Foraging-flight sample sizes by year and nesting colony are listed for each species in Table 3-1, and Figure 3-1 shows the locations of all colonies. Figure 3-3 displays the distribution of foraging-flights by year for Great Egrets. Flight times ranged from 0.2 - 49.0 minutes with a median of 6.4 minutes. Flight distances ranged from 0.1 - 33.3 km, with a median of 3.7 km. A total of 197 or 55% of all Great Egret flights ended within the diked boundary of the lake. However, the likelihood ratio χ^2 test confirmed significant annual variation in the proportions that ended on and off the lake. More flights ended on as opposed to off the lake in all years except 1990, and the 1989 and 1992 on-lake proportions were significantly higher than in 1990 (Table 3-2). Tallies of on- and off-lake flights versus intervals of mean lake stage further confirmed that the proportion of off-lake flights increased as the lake stage dropped below 3.7 m (Table 3-3).

There was also an annual effect on flight distances. The ANOVA of log-transformed flight distances versus year indicated a significant relationship (Table 3-4; $F = 3.60$, df = 3, 352, $P = 0.014$). Bonferroni *t*-test multiple comparisons with the experiment-wise error set at $\alpha = 0.05$ indicated that the mean flight distance in 1989 (2.2 km back-transformed mean) was significantly shorter than in 1990 (3.8 km). With the experiment-wise α level relaxed to 0.10, the difference between 1989 and 1991 (3.2 km) was also considered significant.

Table 3-1. Foraging flight sample sizes (total number of birds followed to landing) by species, year, and nesting colony.

Year	Colony	Great Egret	Snowy Egret	Tricolored Heron	White Ibis
1989	Eagle Bay Island	22	17	1	31
	Moore Haven	50	12	0	12
	Cochran's Pass	0	1	1	30
	Uncle Joe's	17	0	0	0
	Clewiston Spit	0	4	9	0
	Totals	89	34	11	73
1990	Eagle Bay Island	49	38	7	147
	South Fisheating Bay	0	19	5	0
	Clewiston Spit	30	56	31	0
	Totals	79	113	43	147
1991	Taylor Creek	5	0	0	0
	Eagle Bay Island	56	16	0	39
	Okee-Tantie Island	17	0	0	0
	Central Fisheating Bay	30	44	25	0
	Clewiston Spit	46	20	2	0
	Totals	154	80	27	39
1992	Eagle Bay Island	13	1	0	11
	Moore Haven	13	6	0	16
	Clewiston Spit	8	2	0	0
	Totals	34	9	0	27
	Grand Totals	356	236	81	286

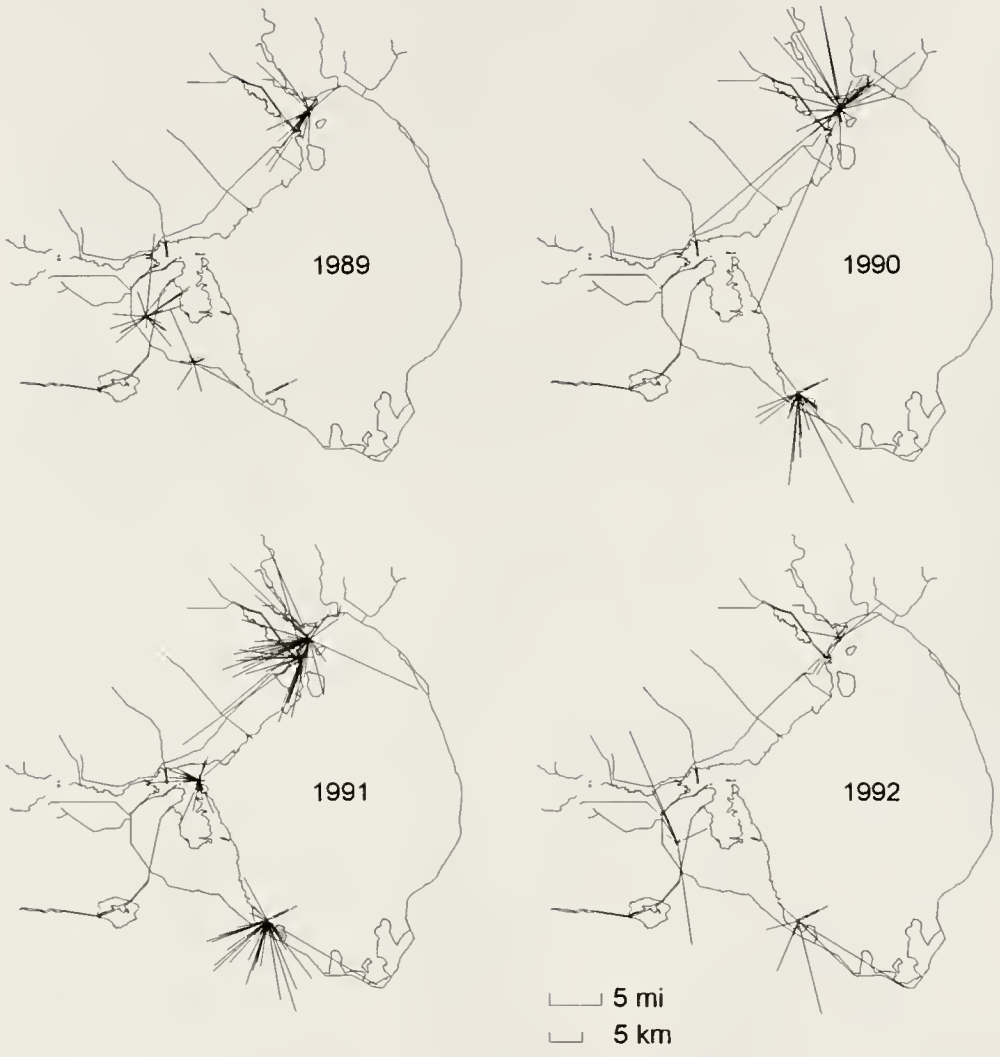


Figure 3-3. Annual distributions of nesting Great Egret foraging flights: 1989-1992.

Table 3-2. Chi-square tests for each species comparing annual proportions of foraging flights that ended on and off the lake.

Year	Destination	Great Egret[a]	Snowy Egret[b]	Tricolored Heron[c]	White Ibis[d]
1989	On	64 (72)[e]	32 (94)	11 (92)	55 (75)
	Off	25	2	1	18
1990	On	33 (42)	104 (92)	43 (96)	107 (73)
	Off	46	9	2	40
1991	On	79 (51)	53 (66)	27 (96)	20 (51)
	Off	75	27	1	19
1992	On	21 (62)	4 (44)	0	12 (44)
	Off	13	5	0	15
Totals	On	197 (55)	193 (82)	81 (95)	194 (68)
	Off	159	43	4	92

[a] Likelihood ratio $\chi^2 = 17.8$, df = 3, $P < 0.001$ (SAS Institute, Inc. 1988); χ^2 multiple comparisons (Fleiss 1981:141) with $\alpha = 0.05$--on-lake proportion significantly greater in 1989 than in 1990 and 1991, and significantly greater in 1992 than in 1990.

[b] Likelihood ratio $\chi^2 = 31.4$, df = 3, $P < 0.001$; multiple comparisons--on-lake proportion significantly greater in 1989 than in 1991, and significantly greater in 1990 than in 1991 and 1992.

[c] No statistical tests for this species; 1990 and 1991 off-lake flights were not followed to completion.

[d] Likelihood ratio $\chi^2 = 14.5$, df = 3, $P = 0.002$; multiple comparisons--on-lake proportion significantly greater in 1990 than in 1991 and 1992.

[e] Numbers in parentheses indicate on-lake percentages.

Table 3-3. Numbers of on and off-lake flights in relation to mean lake stage (m NGVD), with data pooled across years.

Species	Lake Stage	On-lake (%)	Off-lake
Great Egret	≤3.5	24 (42)	33
	3.5-3.8	23 (61)	15
	3.8-4.1	127 (57)	95
	>4.1	23 (59)	16
Snowy Egret	≤3.4	103 (92)	9
	3.4-3.7	19 (100)	0
	>3.7	71 (67)	35
Tricolored Heron	≤3.7	54 (95)	3
	>3.7	27 (96)	1
White Ibis	≤3.5	124 (72)	49
	3.5-3.8	25 (76)	8
	3.8-4.1	21 (84)	4
	>4.1	24 (44)	31

The multiple regression of flight distance versus lake stage, days of rising water, and rainfall totals did not indicate any statistically significant effects ($F = 1.56$, df = 3, 352, $P = 0.199$). However, a positive correlation with days-of-rising-water and a negative correlation with rainfall approached significance (t-test for coefficients, $P = 0.082$ and 0.102, respectively). Thus, although the effects were weak, both rising water and a lack of rainfall during the drought might have forced some Great Egrets to travel longer distances to find suitable foraging habitats. The negative correlation with rainfall was consistent with the finding of an increased proportion of off-lake flights at the lowest lake stages; i.e., when habitats on the lake dried during the drought, birds were forced to search farther--often outside the boundaries of the lake--to find foraging

Table 3-4. Analyses of variance of flight distances (km) versus year for each species, with medians and ranges of flight distances shown for comparison.

	N	Median Flight Distance	Flight Distance Range	Mean Flight Distance[a]	Multiple Comparisons[b]
Great Egret					
1989	89	2.2	0.2-13.0	2.2 ± 1.13	b
1990	79	4.6	0.2-33.3	3.8 ± 1.14	a
1991	154	3.7	0.1-22.9	3.2 ± 1.10	ab[c]
1992	34	3.9	0.2-19.7	2.8 ± 1.22	ab
Snowy Egret					
1989	34	2.0	0.1-9.1	2.0 ± 1.31	a
1990	113	2.1	0.1-23.7	1.9 ± 1.16	a
1991	80	3.5	0.2-29.8	3.3 ± 1.19	a
1992	9	7.8	0.1-12.0	3.7 ± 1.69	a
Tricolored Heron					
1989	11	2.7	0.4-20.3	3.5 ± 1.46	a
1990	43	2.1	0.1-22.3	2.6 ± 1.22	a
1991	27	2.5	0.2-8.1	2.3 ± 1.27	a
White Ibis					
1989	73	4.6	0.3-33.3	4.6 ± 1.15	a
1990	147	2.1	0.1-27.9	2.5 ± 1.11	b
1991	39	3.9	0.5-14.4	3.1 ± 1.22	ab
1992	27	0.7	0.1-9.8	1.0 ± 1.27	c

[a] Back-transformed least squares means and standard errors derived from ANOVA with distances log-transformed (ln[x]).

[b] Means with the same letter cannot be separated using Bonferroni *t*-tests with experiment-wise $\alpha = 0.05$ (see text for overall *F*-test results).

[c] Difference between 1989 and 1991 significant if experiment-wise α relaxed to 0.10.

opportunities. An examination of daily lake stage and rainfall records around the days when the longest flights occurred provided additional evidence that reversals in established surface-water recessions drove at least some birds to travel greater distances to forage. However, the lack of statistically significant regression results suggested that such cases were the exception rather than the rule.

The χ^2 analysis of habitat use versus intervals of mean lake stage is summarized in Table 3-5. Despite a high degree of aggregation, the expected frequencies still remained low in many cells of the table (41% less than five), and therefore a significance test based on the χ^2 probability distribution may not be accurate (e.g., see Sokal and Rohlf 1981: 709 or Fleiss 1981: 25). Normally, one would attempt further aggregation of classes to eliminate the low frequency cells. Reducing the lake stage categories to two--i.e., high and low stage--produced a table with low-frequency cells totaling <20% of the total number of cells (the threshold that elicits a warning in SAS). However, doing so did not affect the overall significance level of the test ($P < 0.001$), nor the primary conclusions that the table suggested. Moreover, the expanded table helped highlight points of transition in the habitat-use trends that were obscured in the collapsed table. I therefore present the expanded table and related statistics in Table 3-5, but emphasize that implied significance levels may overestimate the importance of marginal trends (Sokal and Rohlf 1981: 709).

Previous analyses indicated higher use of off-lake habitats at low lake stages (Table 3-4). The data in Table 3-5 indicate that this trend was due to increased use of only two of three off-lake habitat types--sugar-cane field habitats (AG) and panhandling stations (PANH). The opposite, trend was shown for the third off-lake habitat type--pasture and slough wetlands (PS); i.e., such habitats were used proportionately more

Table 3-5. Chi-square analysis for Great Egrets examining patterns of habitat use in relation to mean lake stage (m NGVD), with data pooled across years.

Lake Stage	Habitat Categories[a]								Total
	AG	PS	PANH	MS-OF	MS-A	MP	MTR	UTR	
≤3.5	12 (21)[b]	8 (14)	13 (23)	20 (35)	0 (0)	3 (5)	0 (0)	1 (2)	57
	6	13	7	8	2	15	4	4	
	5.3	6.3	9.5	19.7	1.6	1.7	3.5	2.1	
3.5-3.8	2 (5)	6 (16)	7 (18)	5 (13)	0 (0)	14 (37)	4 (11)	0 (0)	38
	4	8	4	5	1	10	2	3	
	1.1	1.6	1.7	0.0	1.1	0.7	1.2	2.6	
3.8-4.1	22 (10)	55 (25)	18 (8)	20 (9)	10 (5)	65 (29)	15 (7)	17 (8)	222
	24	49	26	30	6	56	14	15	
	0.2	2.2	0.8	3.3	2.3	0.7	0.1	0.3	
>4.1	3 (8)	10 (26)	3 (8)	3 (8)	0 (0)	11 (28)	3 (8)	6 (15)	39
	4	9	4	5	1	10	2	3	
	0.4	0.5	0.1	1.0	1.1	0.2	0.8	4.3	

Note: Overall likelihood ratio $\chi^2 = 83.4$, df = 21, $P < 0.001$ (SAS Institute, Inc. 1988), indicating that patterns of habitat use varied in response to changing lake stage.

[a] Off-lake: AG - agricultural fields, primarily sugar-cane field ditches and peripheral canals; PS - pasture and slough wetlands; PANH - panhandling stations. On-lake: MS-OF - mixed-submerged and open outer-fringe habitats featuring primarily Hydrilla, Vallisneria, Potamogeton, and Panicum hemitomon in places; MS-A - mixed submerged habitats exploited by aerial foraging; MP - mixed emergent prairie featuring primarily Eleocharis, Panicum, and Nymphaea; MTR - complex middle littoral zone transitional habitats featuring Pontedaria; UTR - upper littoral zone transitional habitats featuring grass/sedge mixes or Polygonum.

[b] Values in descending vertical order: 1) observed count with row percentage in parentheses; 2) expected count--i.e., that which would yield a consistent annual pattern; 3) cell contribution to Pearson χ^2--indicates approximate relative contribution of each count to the overall χ^2 statistic: values above 3.8 indicate a significant contribution ($P \leq 0.05$), values above 2.7 indicate a marginal contribution ($P \leq 0.10$).

at higher stages. In all three cases, the significant change in pattern occurred at the lowest stages (individual cell χ^2 values above 3.8, the $P = 0.05$ threshold for a 1 df χ^2 test of significance). AG and PANH habitats were used more than expected at low stages, and PS habitats were used less than expected at low stages based on the null hypothesis of no association between stage and habitat use.

The second primary trend evident in Table 3-5 is that the relative use of mixed-submerged and outer-fringe habitats (MS-OF) increased significantly at low lake stages. The trends shown for the MS-A habitat type did not contribute significantly to the overall χ^2 statistic. However, the data were nonetheless instructive in that use of this habitat type and foraging strategy was pronounced only at moderately high lake stages, rather than at low lake stages when use of submerged vegetation habitats was generally high. The association with lake stage may be coincidental, however, in that Great Egret use of aerial foraging was facilitated by persistent winds, which happened to be common during the spring of 1991 when the lake stage remained moderate (pers. observ.).

Use of mixed-prairie habitats (MP) was proportionately low at the lowest lake stages because of drying (Table 3-5). Otherwise, mixed prairie habitats were used more than any other single habitat at all other lake stage ranges, but relative use of such habitats declined with increasing lake stage as activity shifted more towards upper transitional habitat types (UTR). The individual cell χ^2 values indicated that changes in the pattern of use of mixed-prairie habitats did not contribute significantly to the overall χ^2 statistic. In combination, these facts indicated that consistent use of mixed-prairie habitats by Great Egrets was not strongly dependent on lake stage levels.

Flight distances averaged significantly shorter in 1989 than in 1990, and insignificantly shorter than in 1991 (Table 3-4); however, the differences did not translate to higher lakewide nest success and productivity (Table 3-6; see Chapter 4 for detailed nest success data). The only indication of support for the research hypothesis (i.e., shorter flight distances should translate to higher success and production) was the comparison of 1989 and 1992 nestling production, but the trend did not hold for the related comparison of nest success. Within years, levels of success and productivity varied by colony. Regressions of colony-specific median flight distances versus levels of nestling-period success and nestling production failed to reveal significant combined-year trends (Fig. 3-4; *t*-test for regression slope coefficients: $t = -0.49$ and 0.65, respectively, df = 8, $P > 0.05$). However, within each year except 1991, the inter-colony trends for nestling-period success were consistent with the research hypothesis (Fig. 3-4). The same was true for 1990 and to a lesser degree 1992 nestling production, but the trend did not hold for 1989 nestling production. The lower success and production colony was usually the Eagle Bay Island colony--and the nearby Okee-Tantie Island colony in 1991 (Fig. 3-1). This consistency, combined with the fact that the cross-year trend for Eagle Bay Island was slightly positive, suggested that there may have been other factors operating at Eagle Bay Island (and Okee-Tantie Island) that led to the consistently lower success. Specifically, the northern colonies---Eagle Bay Island the primary example--were the first occupied each year, and consequently the birds nesting there were more subject to the negative impact of late-winter cold fronts (Chapters 4, 5).

I also examined the relationship between foraging-flight distances and lakewide rates of nest failure by tallying failures among marked nests (Chapter 4) and calculating

Table 3-6. Annual mean foraging flight distances compared to lakewide estimates of nestling-period success and nestling production by species.

	Mean Flight Distance (km)[a]	Nest Success[b]	Nestlings Per Hatched Nest[c]	Number Hatched Nests
Great Egret				
1989	2.2	0.68	1.6	54
1990	3.8	0.82	1.9	126
1991	3.2	0.91	1.8	127
1992	2.8	0.75	1.3	84
Snowy Egret				
1989	2.0	0.78	2.0	59
1990	1.9	0.91	2.1	94
1991	3.3	0.80	1.9	87
1992	3.7	0.56	2.0	26
Tricolored Heron				
1989	3.5	0.89	1.6	19
1990	2.6	0.86	1.8	56
1991	2.3	0.86	1.8	72
White Ibis				
1989	4.6	0.87	1.6	29
1990	2.5	0.80	1.4	56
1991	3.1	0.64	1.0	58
1992	1.0	0.83	1.2	58

[a] Back-transformed least squares means derived from ANOVA (see Table 3-4) with distances log-transformed (ln[x]).

[b] Percentages of hatched nests that produced at least one 21-day old nestling (14-day for White Ibises); Mayfield estimates for 1989-1991, standard percent-survived or Apparent estimate for 1992 (see Chapter 4 for details).

[b] Annual means: 21-day old nestlings for Great Egrets, Snowy Egrets, and Tricolored Herons; 14-day old nestlings for White Ibises.

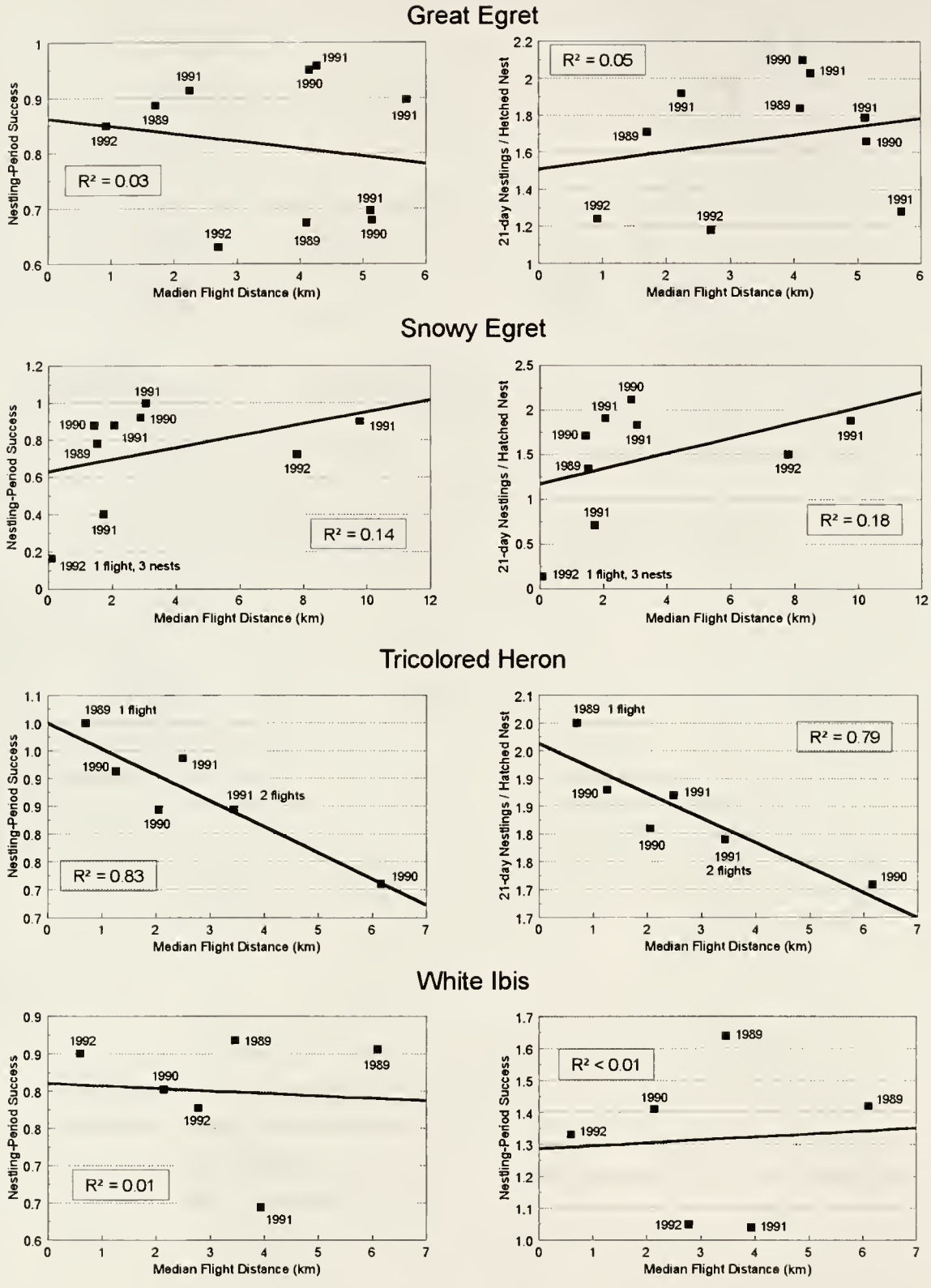


Figure 3-4. Colony-specific estimates of nestling-period success (Mayfield estimates for 1989-1991, standard percent-survived estimates for 1992) and nestling production in hatched nests in relation to median foraging-flight distances.

mean flight distances (standard means) for successive 15-day periods during each nesting season. The resulting regression suggested a slight positive trend, but the relationship was far from significant (Fig. 3-5; *t*-test for regression slope coefficient: t = 0.64, df = 23, $P > 0.05$). Thus, although there was some evidence of a negative correlation between flight distances and colony-specific nest success within years, overall the data were equivocal, suggesting that the productivity of Great Egret nesting efforts was not greatly affected by changes in the energetic or logistic demands of foraging flights.

Snowy Egrets. I followed 236 Snowy Egrets from six colony sites during the study period (Table 3-1). Figure 3-6 displays the distribution of flights by year. Flight times ranged from 0.1 - 62.4 minutes with a median of 4.7 minutes. Flight distances ranged from 0.1 - 29.8 km, with a median of 2.8 km. A total of 193 or 82% of all Snowy Egret flights ended within the diked boundaries of the lake. As for Great Egrets, a likelihood ratio χ^2 test confirmed highly significant annual variation in the proportions that ended on and off the lake; however, the pattern of variation differed from that shown for Great Egrets (Table 3-2). Most Snowy Egret flights ended on the lake in 1989 and 1990, but the on-lake proportion declined significantly in 1991, and more of the relatively few flights monitored in 1992 ended off the lake than on.

The proportion of off-lake flights increased as the lake stage rose above 3.7 m, opposite to the trend shown for Great Egrets (Table 3-3). The ANOVA of log-transformed flight distances versus year indicated that annual effects only approached significance (Table 3-4; F = 2.20, df = 3, 232, P = 0.088). However, the trend in mean flight distances by year was consistent with the data for proportions of on- and off-lake flights; i.e., flight distances averaged progressively longer in 1991 (3.3 km back-

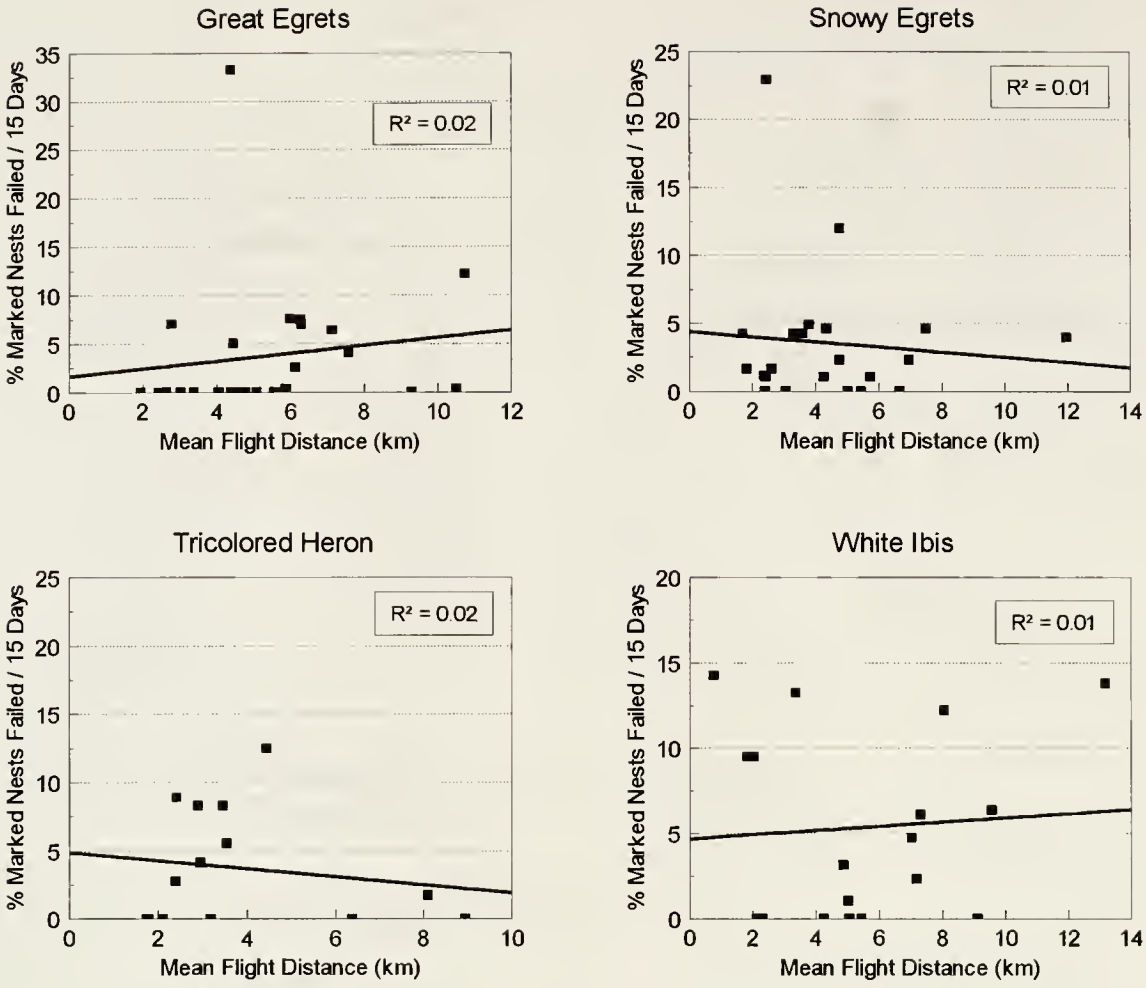

Great Egrets
% Marked Nests Failed / 15 Days
Mean Flight Distance (km)
R² = 0.02
Snowy Egrets
% Marked Nests Failed / 15 Days
Mean Flight Distance (km)
R² = 0.01
Tricolored Heron
% Marked Nests Failed / 15 Days
Mean Flight Distance (km)
R² = 0.02
White Ibis
% Marked Nests Failed / 15 Days
Mean Flight Distance (km)
R² = 0.01

Figure 3-5. Plots by species of the percentages of marked nests (see Chapter 4) that failed--summed over 15-day periods--versus mean foraging-flight distances.

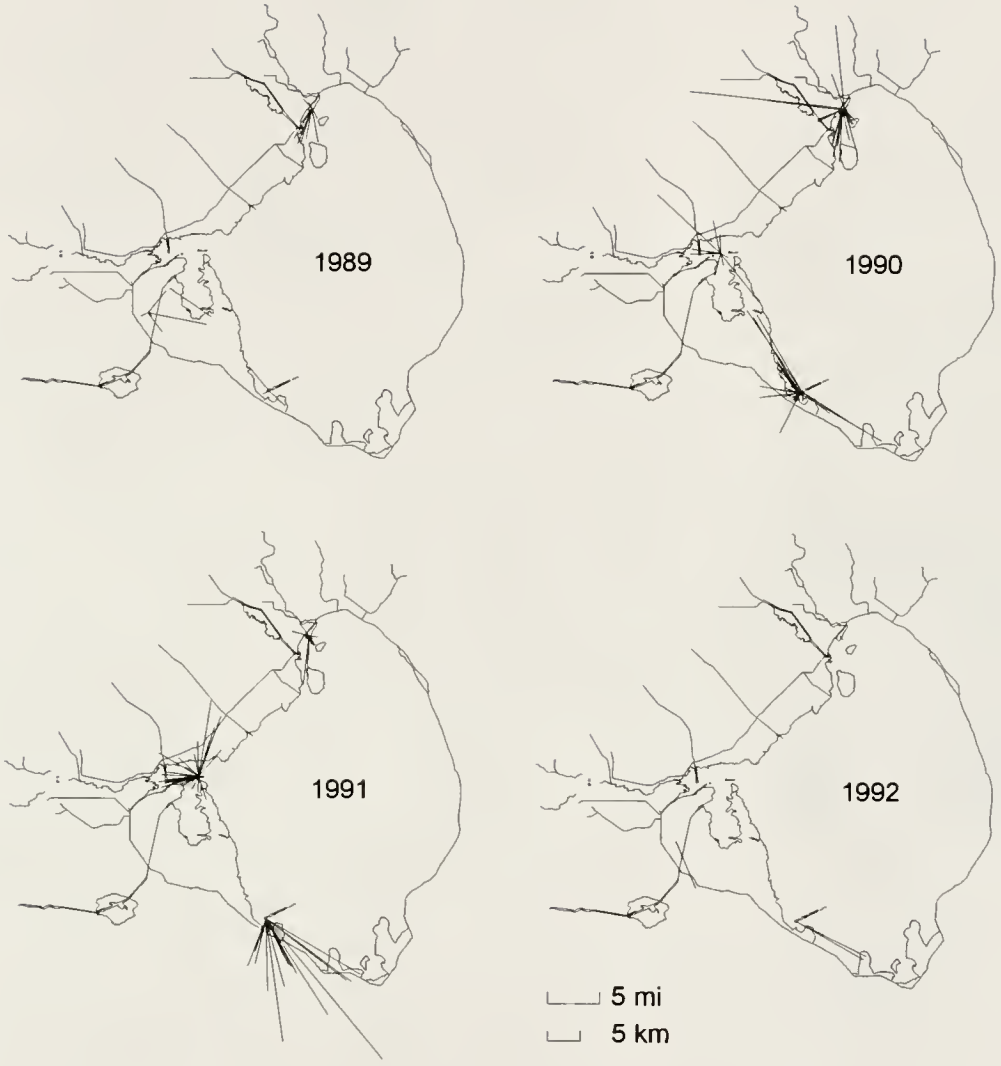


Figure 3-6. Annual distributions of nesting Snowy Egret foraging flights: 1989-1992.

transformed mean) and 1992 (3.7 km) as the proportion of off-lake flights increased (2.0 km in 1989, 1.9 km in 1990).

The multiple regression analysis of flight distances versus hydrologic variables revealed no significant interactions, significant positive correlations of flight distance with mean lake stage (t-test for coefficient, $P = 0.010$) and 30-day rainfall ($P = 0.034$), and an insignificant negative correlation with days-of-rising-water ($P = 0.107$; overall $F = 3.11$, df = 3, 232, $P = 0.027$). The R^2 for the model was very low (0.039), indicating that although Snowy Egret flight distances averaged slightly longer at high lake stages and during periods of high rainfall, hydrologic variation was not a strong determinant of foraging-flight distances.

The lake stage and habitat categories considered in the χ^2 analysis of habitat use differed from those considered in the Great Egret analysis (Table 3-7). The PANH and MTR classes were not used by Snowy Egrets, and use of the specific Hydrilla-mat and lotus (HM-LOT) subcategory of MS-OF habitats was high enough to warrant distinction. In addition, I reduced the stage categories to three because I had less high-stage data for Snowy Egrets (smaller species nest later in the season when water levels are generally lower; Chapter 4). The expected frequencies were low in most cells of the middle stage category, and collapsing the stage categories to two eliminated the potential problem with χ^2 significance levels. However, as with Great Egrets, the adjustment did not change the significance level of the overall test ($P < 0.001$) nor appreciably alter the primary conclusions, but did further obscure points of transition. Therefore, again I present in Table 3-7 an expanded version with more low frequency cells than is ideal, but believe that the strength of the indicated patterns is consistent with a highly significant finding.

Table 3-7. Snowy Egret habitat selection in relation to mean lake stage (m NGVD), with data pooled across years.

Lake Stage	Habitat Categories[a]							Total
	AG	PS	MS-OF	HM-LOT	MS-A	MP	UTR	
≤3.4	2 (2)[b]	7 (6)	69 (62)	20 (18)	7 (6)	5 (4)	2 (2)	112
	11	9	39	22	15	11	4	
	7.7	0.6	23.6	0.2	4.0	3.5	1.2	
3.4-3.7	0 (0)	0 (0)	11 (58)	1 (5)	1 (5)	5 (26)	1 (5)	19
	2	2	7	4	2	2	1	
	1.9	1.6	3.0	2.0	0.9	4.9	0.1	
>3.7	22 (21)	13 (12)	2 (2)	26 (25)	23 (22)	14 (13)	6 (6)	106
	11	9	37	21	14	11	4	
	11.8	1.8	32.8	1.2	6.0	1.0	1.0	

Note: Overall likelihood ratio $\chi^2 = 136.0$, df = 12, $P < 0.001$ (SAS Institute, Inc. 1988), indicating that patterns of habitat use varied in response to changing lake stage.

[a] Off-lake: AG - agricultural fields, primarily sugar-cane field ditches and peripheral canals; PS - pasture and slough wetlands. On-lake: MS-OF - mixed-submerged and open outer-fringe habitats featuring primarily Hydrilla, Vallisneria, Potamogeton, and Najas; HM-LOT - thick, floating mats of Hydrilla mixed with Eichhornia and Lemna, and thick Hydrilla mixed with Nelumbo; MS-A - mixed submerged habitats exploited by aerial foraging; MP - mixed emergent prairie featuring primarily Eleocharis, Panicum, and Nymphaea; UTR - upper littoral zone transitional habitats featuring grass/sedge mixes or Polygonum or flooded Ipomea vines.

[b] Values in descending vertical order: 1) observed count with row percentage in parentheses; 2) expected count--i.e., that which would yield a consistent annual pattern; 3) cell contribution to Pearson χ^2--indicates approximate relative contribution of each count to the overall χ^2 statistic: values above 3.8 indicate a significant contribution ($P \leq 0.05$), values above 2.7 indicate a marginal contribution ($P \leq 0.10$).

Based on the null hypothesis of no association between lake stage and habitat use, both classes of off-lake habitats were used more than expected only at high lake stages (Table 3-7). However, only the trend for AG habitats (primarily sugar cane field ditches and canals) contributed significantly to the overall χ^2 statistic. The strong shift

to using AG habitats at high lake stages was the second most prominent trend indicated in the table. Use of pasture and slough habitats (PS) was almost as high as expected at low stages, whereas AG habitats were used significantly less than expected at low stages. The only habitat type that Snowy Egrets used significantly more than expected at low stages was mixed-submerged and outer-fringe habitats (MS-OF). Furthermore, the magnitude of the low-stage cell χ^2 value suggested (but did not confirm because habitat availability was not considered) a strong preference for these habitats. Snowy Egrets continued to rely on submerged vegetation habitats at high lake stages, but shifted to using aerial foraging techniques (MS-A) and HM-LOT habitats. The latter habitat class featured thick mats of Hydrilla, floating mats of water hyacinth, and large surface leaves of lotus that provided support in water too deep for wading (Chapter 2). The sample sizes for the moderate-stage category were relatively small, but like Great Egrets, Snowy Egrets used mixed-prairie habitats (MP) significantly more often than expected at moderate lake stages, and to a lesser degree at high stages. Trends for the upper-transitional habitat (UTR) type were not pronounced, but again like Great Egrets, Snowy Egrets used these habitats most at the highest lake stages.

As was generally true for Great Egrets, variation in Snowy Egret flight distances did not appear to influence lakewide levels of nestling-period success and nestling production (Table 3-6). The only possible exception was in 1992 when the mean flight distance was longest and nestling-period success was lowest; however, both the flight (Table 3-1) and nest sample sizes (Table 3-6) were low in 1992, reducing the reliability of the estimates. Moreover, the 1992 estimate of nestling production was not particularly low, and regressions of colony-specific median flight distances versus levels

of nestling period success and nest productivity indicated weak positive rather than negative associations (Fig. 3-4; *t*-tests for regression slope coefficients: $t = 1.07$ and 1.25, respectively, df = 7, $P > 0.05$). A regression of marked-nest failures versus mean flight distances (standard means) also showed no significant trend (Fig. 3-5; *t*-test for regression slope coefficient: $t = -0.39$, df = 20, $P > 0.05$).

Tricolored Herons. I successfully followed only 82 Tricolored Herons from 1989-1991, and did not follow any birds in 1992. Thus, the results for this species should be considered the most tentative. Moreover, I succeeded in following only one Tricolored Heron to an off-lake destination--a small grassy ditch near a sugar cane field. Observations suggested that Tricolored Herons were less likely than other species to travel off-lake to forage, but I failed to complete following efforts for three other individuals that landed somewhere in the sugar cane fields southwest of the lake (Fig. 3-7). I listed the four off-lake observations in Tables 3-2 and 3-3, and included the flights in the illustrations of flight distributions (Fig. 3-7), but the remainder of the presentation deals only with on-lake data.

Flight times ranged from 0.3 - 50.0 minutes with a median of 4.0 minutes. Flight distances ranged from 0.1 - 22.3 km with a median of 2.4 km. Based on log-transformed means, flight distances averaged longest in 1989 (3.5 km back-transformed mean), intermediate in 1990 (2.6 km), and shortest in 1991 (2.3 km), but none of the differences were statistically significant (Table 3-4; ANOVA $F = 0.406$, df = 2, 76, $P = 0.668$). The multiple regression analysis of flight distances versus hydrologic variables also revealed no significant relationships ($F = 0.13$, df 3, 77, $P = 0.940$).

Figure 3-7. Annual distributions of nesting Tricolored Heron foraging flights: 1989-1992.

For analyses of habitat use versus lake stage, two lake stage categories summarized the primary trends and reduced the number of low frequency cells (Table 3-8). The number of low frequency cells still remained unacceptably high, however, and therefore the indicated significance levels are suspect. Nonetheless, some pronounced trends were evident, the most prominent of which concerned the relative use of two types of outer littoral-zone habitat. As with other species, mixed-submerged and outer-fringe habitats (MS-OF) were of primary importance at low lake stages, but in general were used less than expected at high stages. However, as was true for Snowy Egrets, at high lake stages Tricolored Herons continued to use thick, surface mats of Hydrilla mixed with floating hyacinth (HM-HYC) for support in habitats too deep for wading. Moreover, regardless of the lake stage, Tricolored Herons consistently chose to forage in deep-water Hydrilla flats where the large surface leaves of intermixed lotus plants provided the necessary support (H-LOT). The only other apparently significant trend was that Tricolored Herons, like other species, increasingly turned to upper transitional habitat mixes at high lake stages.

I did not monitor any Tricolored Heron flights in 1992, and the flight and nest success data for 1989 were not well matched (only one flight monitored from one of two colonies in which nests were marked). Consequently, I had little data on which to base comparisons of flight distances and nest success and productivity. Moreover, annual, lakewide estimates of Tricolored Heron nest success and productivity did not vary significantly over the course of the study (Chapter 4). The small difference between 1990 and 1991 lakewide mean flight distances did not translate to similar differences in nest success and productivity, but longer flights were matched with slightly lower nestling production in 1989 (Table 3-6). In addition, colony-specific

Table 3-8. Tricolored Heron habitat selection in relation to mean lake stage (m NGVD), with data pooled across years.

Lake Stage	Habitat Categories[a]					Total
	MS-OF	HM-HYC	HLOT	MP	UTR	
≤3.7	38 (70)[b]	0 (0)	6 (11)	6 (11)	4 (7)	54
	25	9	7	4	9	
	6.3	8.7	0.24	1.0	2.5	
>3.7	0 (0)	13 (48)	5 (19)	0 (0)	9 (33)	27
	13	4	4	2	4	
	12.7	17.3	0.5	2.0	5.0	

Note: Overall likelihood ratio $\chi^2 = 71.9$, df = 4, $P < 0.001$ (SAS Institute, Inc. 1988), indicating that patterns of habitat use varied in response to changing lake stage.

[a] All habitats on-lake: MS-OF - mixed-submerged and open outer-fringe habitats featuring primarily Hydrilla, Vallisneria, Potamogeton, and Najas; HM-HYC - thick, floating mats of Hydrilla mixed with Eichhornia and Lemna; HLOT - thick Hydrilla mixed with Nelumbo; MP - mixed emergent prairie featuring primarily Eleocharis, Panicum, and Nymphaea; UTR - upper littoral zone transitional habitats featuring grass/sedge mixes or Polygonum or flooded Ipomea vines.

[b] Values in descending vertical order: 1) observed count with row percentage in parentheses; 2) expected count--i.e., that which would yield a consistent annual pattern; 3) cell contribution to Pearson χ^2--indicates approximate relative contribution of each count to the overall χ^2 statistic: values above 3.8 indicate a significant contribution ($P \leq 0.05$), values above 2.7 indicate a marginal contribution ($P \leq 0.10$).

estimates of nest success and nestling production varied more than the lakewide averages suggested, and combined-year regressions of these statistics versus median flight distances showed strong negative trends (Fig. 3-4; *t*-tests for regression slope coefficients: $t = -4.46$ and 3.83, respectively, df = 4, $P < 0.01$). However, a regression of marked nest failure rates versus mean flight distances (standard means) showed a slight negative trend (Fig. 3-5; *t*-test for regression coefficient: $t = -0.55$, df = 12, $P > 0.05$), which was inconsistent with the previous finding. Thus, there was colony-

specific evidence that the demands of longer foraging flights increased the chance of nest failure and reduced the productivity of Tricolored Herons. However, the data were limited in scope and overall the messages were mixed; therefore, I consider the results tentative.

White Ibis. I followed 286 White Ibises from three colony sites over the four-year study period. Figure 3-8 displays the distribution of flights by year. Flight times ranged from 0.2-52.1 minutes with a median of 3.8 minutes. Flight distances ranged from 0.1-33.3 km, with a median of 2.7 km. A total of 194 or 68% of all flights ended within the diked boundaries of the lake. A likelihood ratio χ^2 test again indicated significant ($P = 0.002$) annual variation in the proportions ending on- and off-lake (Table 3-2). The data for White Ibises followed the same trend shown for Snowy Egrets; i.e., the proportion of off-lake flights increased from 1989 through 1992. Multiple comparisons indicated that a significantly higher proportion of flights ended on the lake in 1990 (73%) than in 1991 (51%) and 1992 (44%). The proportion of on-lake flights was even higher in 1989 (75%), but the small sample sizes precluded the demonstration of significant differences for comparisons with 1991 ($P = 0.112$) and 1992 ($P = 0.086$). Comparisons by month within years and tallies of on- and off-lake flights versus intervals of lake stage (Table 3-3) indicated that the proportion of off-lake flights increased at both low (below 3.7 m) and high (above 3.9 m) lake stages.

The ANOVA of log-transformed flight distances versus year indicated a highly significant annual effect (Table 3-4; $F = 10.5$, df = 3, 282, $P < 0.001$, $R^2 = 0.100$). Bonferroni *t*-test multiple comparisons confirmed that the mean flight distance in 1989 (4.6 km back-transformed mean) was significantly longer than in 1990 (2.5 km), and that the mean distance in 1992 (1.0 km) was significantly shorter than in all other years

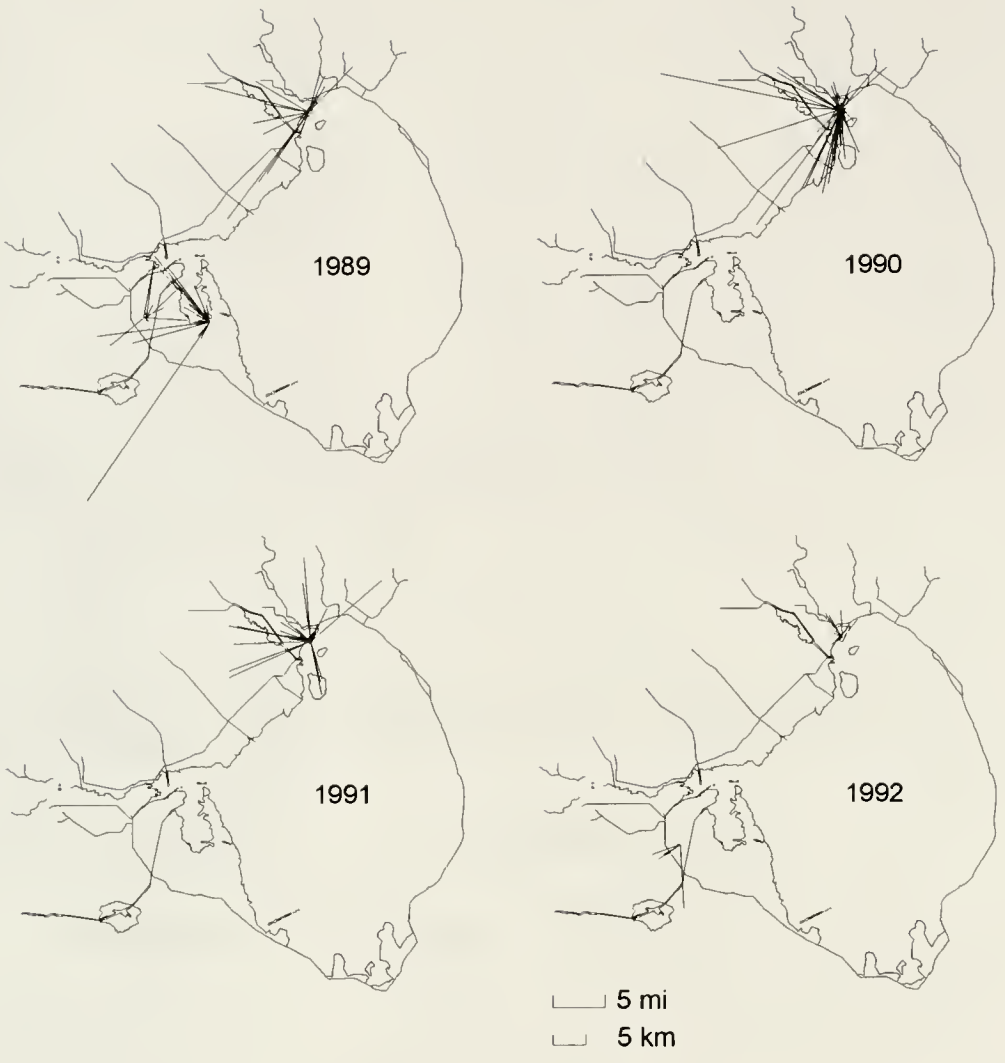


Figure 3-8. Annual distributions of nesting White Ibis foraging flights: 1989-1992.

(3.1 km in 1991). This indicated that a higher annual proportion of off-lake flights did not necessarily translate to a higher mean flight distance. However, within years the mean distance for off-lake flights ranged from 2.0-2.6 times higher than the mean for on-lake flights.

The multiple regression analysis (overall $F = 6.272$, df = 4, 281, $P < 0.001$) revealed that, all else equal, flight distances averaged longer at higher stages (significant positive correlation; *t*-test for coefficient, $P = 0.011$). The analysis also showed that reversals in established drying trends generally led to longer flights, but that flight distances declined in response to the persistence of a steady rising water trend. The latter details were reflected by significant positive correlations between flight distance and the days-of-rising-water and rainfall variables ($P < 0.002$), and a significant negative correlation with the days-of-rising-water by rainfall interaction term ($P < 0.001$). In other words, an increase in either variable (rising water) led to longer flights if the change followed an extended period of low rainfall and receding water (i.e. both variables previously low, contribution of interaction term relatively unimportant), but led to shorter flights if the change insured the persistence of an established rising water trend (i.e., both variables already high, contribution of interaction term dominant). The R^2 for the model was low (0.082), indicating that the hydrologic variables explained a significant but small portion of the variance in the data. Examining specific stage and rainfall measurements around dates when the longest flights occurred further confirmed that inconsistent rising trends and especially abrupt reversals to rising water were likely causes of occasional long flights.

Four habitat and four lake stage categories effectively summarized the primary trends in habitat use, and resulted in an acceptable distribution of data (Table 3-9).

Table 3-9. White Ibis habitat selection in relation to mean lake stage (m NGVD), with data pooled across years.

Lake Stage	Habitat Categories[a]				Total
	OFF	MS-OF	MP	UTR	
≤3.5	49 (28)[b]	103 (60)	11 (6)	10 (6)	173
	56	65	32	20	
	0.79	21.7	13.8	5.0	
3.5-3.8	8 (24)	5 (15)	20 (61)	0 (0)	33
	11	12	6	4	
	0.64	4.5	31.5	3.8	
3.8-4.1	4 (16)	0 (0)	11 (44)	10 (40)	25
	8	9	5	3	
	2.0	9.4	8.8	17.6	
>4.1	31 (56)	0 (0)	11 (20)	13 (24)	55
	18	21	10	6	
	10.0	20.8	0.1	7.0	

Note: Overall likelihood ratio $\chi^2 = 171.1$, df = 9, $P < 0.001$ (SAS Institute, Inc. 1988), indicating that patterns of habitat use varied in response to changing lake stage.

[a] Off-lake: OFF - all off-lake habitats combined; mostly flooded pasture, pasture ponds and ditches, and pocket and slough wetlands, plus some sugar-cane field ditches and cattle feedlots. On-lake: MS-OF - mixed-submerged and open outer-fringe habitats featuring primarily Hydrilla and Vallisneria variably mixed with Eichhornia, Hydrocotyle, Nelumbo, and Scirpus; MP - mixed emergent prairie featuring primarily Eleocharis, Panicum, and Nymphaea; UTR - upper littoral zone transitional habitats featuring grass/sedge mixes, Polygonum, or flooded Ipomea vines.

[b] Values in descending vertical order: 1) observed count with row percentage in parentheses; 2) expected count--i.e., that which would yield a consistent annual pattern; 3) cell contribution to Pearson χ^2--indicates approximate relative contribution of each count to the overall χ^2 statistic: values above 3.8 indicate a significant contribution ($P \leq 0.05$), values above 2.7 indicate a marginal contribution ($P \leq 0.10$).

Trends similar to those shown for other species were evident, and a highly significant likelihood ratio χ^2 confirmed strong a strong association between lake stage and patterns of habitat use. The single off-lake habitat category (OFF) included a diverse mix of pasture, cattle feedlot, and shallow ditch and slough habitats, but the trend was consistent for all subcategories and so I lumped them together for the final presentation. As shown previously, some birds used off-lake habitats each year, but a greater proportion of the flights ended off-lake in 1992 when the lake stage was highest (Table 3-3). This trend was reflected in Table 3-9 as a highly significant shift towards off-lake habitats at high stages. Use of mixed prairie habitats (MP) was particularly pronounced at moderate stages, whereas such habitats were used less than expected at low stages when--as was true for other species--the focus of attraction was mixed submerged and outer fringe habitats (MS-OF). White Ibises foraged in mixed-submerged and outer fringe habitats much less frequently than Snowy Egrets and Tricolored Herons, but like all species shifted to such habitats at the height of the drought when upper-elevation habitats were largely dry and prey were heavily concentrated in the submergent zone (Chapter 2). Conversely, besides increasing their use of off-lake habitats at high lake stages, ibises also concentrated in upper transitional habitats (UTR) on the lake.

Comparisons of annual mean flight distances versus estimates of lakewide nest success and productivity revealed no consistent trends (Table 3-6). Combined-year regressions of colony-specific estimates of nestling-period success and nestling production versus median flight distances also revealed no significant trends (Fig. 3-4; t-tests for regression slope coefficients: t = -0.15 and 0.15, respectively, df = 4, $P >$ 0.05). However, as was true for Great Egrets, the intra-annual trends for 1989 and

1992 (the only years in which two or more colonies were studied) were consistent with the research hypothesis of decreased success and production with increasing flight distances. The regression of marked-nest failure rates versus mean flight distances (standard means) also revealed a slight positive trend consistent with the research hypothesis, but the trend was far from significant (*t*-test for regression slope coefficient: $t = 0.29$, df = 16, $P > 0.05$). Thus, the evidence again suggested that variation in foraging-flight distances did not influence levels of nest success and productivity in any consistent way or to a significant degree.

Foraging Sociability

Great Egrets were the least likely to travel to foraging sites in groups; only 9% of the birds followed departed the colonies with one or more traveling companions (Table 3-10). Tricolored Herons and Snowy Egrets were significantly more likely than Great Egrets to depart in groups (19% and 26% of all birds, respectively), but White Ibises were the only species in which a majority left in groups (64% of all birds; Table 3-10). Moreover, when White Ibises traveled in groups, the size of the group averaged larger than those of other species; however, the only statistically significant difference was between White Ibises and Snowy Egrets. The mean Great Egret group size was even smaller than for Snowy Egrets, but because the group sample size was smaller, the difference relative to White Ibises was significant only if the experiment-wise α was relaxed to 0.10 (Table 3-10). Snowy Egrets and Tricolored Herons were significantly more likely than Great Egrets to depart in groups; however, more of the Snowy Egret and especially Tricolored Heron groups dispersed before landing (Table 3-10). The result was that only 2% of the Tricolored Herons landed with a traveling companion,

Table 3-10. Chi-square tests examining species' tendencies to travel in groups to foraging locations.

Species	Total Birds Departed	Total Birds Followed to Landing	Total Birds Departed in Groups[a]	Mean Group Size[b]	Maximum Group Size	% Groups Dispersed Before Landing	% Groups Partially Dispersed Before Landing
Great Egret	357	356	32 (9)	2.2 ± 0.79 (14)	4	29	0
Snowy Egret	242	237	64 (26)	2.3 ± 1.08 (27)	4	41	0
Tricolored Heron	84	81	16 (19)	2.5 ± 1.18 (6)	5	83	0
White Ibis	324	286	208 (64)	3.0 ± 1.05 (62)	11	31	19

[a] Likelihood ratio $\chi^2 = 259.6$, df = 3, $P < 0.001$ (SAS Institute, Inc. 1988); χ^2 multiple comparisons (Fleiss 1981:141) with $\alpha = 0.05$--White Ibises significantly more likely than others to depart in groups, Great Egrets significantly more likely to depart alone. Values in parentheses indicate percent of total.

[b] ANOVA with log-transformed (ln[x]) group sizes: $F = 3.75$, df = 3, 105, $P = 0.013$; Bonferroni *t*-test multiple comparisons with $\alpha = 0.05$--White Ibis groups significantly larger than Snowy Egret groups (difference between White Ibises and Great Egrets significant if $\alpha = 0.10$)(Wilkinson 1990). Birds that travelled alone were excluded from this analysis. The means and standard errors given represent back-transformed least squares estimates. The lower numbers in parentheses indicate group sample sizes.

compared to 7% of the Great Egrets and 15% of the Snowy Egrets. Fifty percent of the White Ibis groups also dispersed to some degree before landing, but still 41% of the ibises followed landed with one or more of their original traveling companions.

A majority of individuals of all species landed either with or near other foraging birds (Table 3-11). White Ibises were the most likely to land in the immediate vicinity of other birds, and rarely landed in areas devoid of other birds. Moreover, the groups that ibises joined averaged significantly larger than those of other species (Table 3-11). Snowy Egrets also usually joined other birds or at least landed near other birds. Great Egrets were less likely to land in the immediate vicinity of other birds, but still usually landed at least near other birds rather than alone. Tricolored Herons were more likely to land alone than in the immediate vicinity of other birds, but still usually chose habitats already occupied by one or more birds. The size of the groups that Great Egrets and Snowy Egrets joined averaged significantly smaller than those joined by White Ibises, but significantly larger than the groups joined by Tricolored Herons (Table 3-11).

Tricolored Herons that landed with or near other foraging birds were about as likely as not to join conspecifics (54% did, 46% did not), but compared to other species, Tricolored Herons were the least likely to join conspecifics (Table 3-11). This tendency was the dominant contributor to a highly significant χ^2 test statistic for the comparison of species' tendencies. Great Egrets that joined other birds were also significantly less likely than Snowy Egrets and White Ibises to join conspecifics, but nonetheless the majority did. In addition, 43% of the Snowy Egrets and White Ibises, and 37% of the Great Egrets that landed with other birds joined or landed near only other conspecific individuals, but the proportion dropped to only 17% for Tricolored Herons. Great Egrets and Tricolored Herons that joined mixed-species aggregations joined flocks that

Table 3-11. Chi-square tests examining species' tendencies to join other birds at foraging sites, and an ANOVA examining species' differences with regards to the size of the feeding flocks each tended to join.

Species	Total Birds Followed[a]	Landed Alone[a]	Landed Near Others[a]	Landed With Flock[a]	% Joining Birds That Landed Near/With Conspecifics[b]	Mean Size of Feeding Flock Joined[c]
Great Egret	356	102 (29) 66 19.6	59 (16) 51 1.2	195 (55) 239 20.3	87	11.7 ± 2.46 254 1-650
Snowy Egret	237	22 (9) 44 11.0	38 (16) 34 0.5	177 (75) 159 2.0	96	15.7 ± 1.13 215 1-955
Tricolored Heron	81	35 (43) 15 26.6	16 (20) 12 1.6	30 (37) 54 10.9	54	5.2 ± 1.29 45 1-100
White Ibis	286	19 (7) 53 21.8	25 (9) 41 6.3	242 (84) 192 13.1	97	30.9 ± 1.11 267 1-735

[a] Likelihood ratio χ^2 test of species-specific proportions: $\chi^2 = 124.6$, df = 6, $P < 0.001$, indicating that species differed significantly in their tendency to join other birds at foraging sites (SAS Institute, Inc. 1988). Values for each species and category in descending vertical order: 1) observed count with row percentage in parentheses; 2) expected count--i.e., that which would yield a consistent annual pattern; 3) cell contribution to Pearson χ^2--indicates approximate relative contribution of each count to the overall χ^2 statistic: values above 3.8 indicate a significant contribution ($P \leq 0.05$), values above 2.7 indicate a marginal contribution ($P \leq 0.10$).

[b] Likelihood ratio χ^2 test of species-specific proportions: $\chi^2 = 74.0$, df = 3, $P < 0.001$ (SAS Institute, Inc. 1988); χ^2 multiple comparisons (Fleiss 1981:140-141) with $\alpha = 0.05$--Great Egrets and especially Tricolored Herons significantly less likely than other species to join conspecifics.

[c] ANOVA with log-transformed (ln[x]) flock sizes: $F = 63.9$, df = 3, 777, $P < 0.001$; Bonferroni t-test multiple comparisons with $\alpha = 0.05$--White Ibises tended to join significantly larger flocks than all other species, and Snowy Egrets and Great Egrets tended to join significantly larger flocks than Tricolored Herons (Wilkinson 1990). Values for each species in descending vertical order: back-transformed least squares means and standard errors; sample size; range of flock sizes.

included Snowy Egrets (73 and 63% of the birds, respectively) more often than flocks that included White Ibises (54 and 29%). Snowy Egrets and White Ibises usually joined flocks that included conspecifics, but White Ibises joined flocks that included Snowy Egrets (67% of the birds that joined mixed flocks) more often than Snowy Egrets joined flocks that included White Ibises (50%).

Discussion

Foraging-Flight Dynamics, Patterns of Habitat Use, and Nest Productivity

The mean flight distances recorded during this study--whether study-wide, annual lakewide, or colony-specific estimates--usually ranked moderate or low in comparison to estimates from studies conducted in the Everglades and other regions of the United States (Table 3-12). The longest Great Egret, Tricolored Heron, and White Ibis flights were similar to those documented in other studies, but the longest Snowy Egret flight was less than half as long as the longest flight documented by Bancroft et al. (1990, 1994) during a period of large-scale nest abandonment. The latter authors discovered that nest failure increased among several species when foraging-flight distances extended to 25-30 km and beyond. Similarly, Frederick and Collopy (1988) noted that White Ibis nest failure increased when foraging-flight distances extended to about 25 km. In both cases, the authors believed that large-scale reversals to rising water were to blame for the increasing travel distances and colony failures. The evidence I gathered also confirmed that reversals in established drying trends due to high rainfall probably led to increasing flight distances among all species, but a statistically significant association was shown only for Snowy Egrets and White Ibises. Furthermore, few of the birds I followed traveled as far as 25-30 km, and with the

Table 3-12. Nesting adult mean and maximum foraging-flight distances derived from various studies.

Species	Source	Location	Years	N	Mean Distance	Maximum Distance
Great	Custer and Osborn 1978	Newport River Estuary, NC	1976	144	3.6	≅ 27
Egret	Thompson 1978	Upper Mississippi River	1978	18	8.6	35.2
	Frederick and Collopy 1988	Everglades, FL	1986-87	149	4.8	≅ 22
	Bancroft et al. 1990	Everglades, FL	1987-89	132	6.5	31.6
	Frederick 1993	Everglades, FL	1992	3	3.9	≅ 5
	This study	Lake Okeechobee, FL	1989-92	356	5.2	33.3
Snowy	Custer and Osborn 1978	Newport River Estuary, NC	1976	37	3.7	≅ 19
Egret	Frederick and Collopy 1988	Everglades, FL	1986-87	16	9.6	≅ 18
	Bancroft et al. 1990	Everglades, FL	1987-89	284	14.1	65.7
	This study	Lake Okeechobee, FL	1989-92	237	4.3	29.8
Tricolored	Custer and Osborn 1978	Newport River Estuary, NC	1976	81	2.6	≅ 13
Heron	Bancroft et al. 1990	Everglades, FL	1987-89	309	7.6	26.7
	This study	Lake Okeechobee, FL	1989-92	81	5.1	22.3
White	Bateman 1970	Alabama	1969	3[a]	10.3	22.9
Ibis	Kushlan 1976	Everglades, FL	1972-75	--	--	≅ 44
	Custer and Osborn 1978	Newport River Estuary, NC	1976	138	1.6	6.7
	Bildstein et al. 1990	Coastal South Carolina	1979-86	--	--	≅ 40
	Frederick and Collopy 1988	Everglades, FL	1986-87	191	8.4	≅ 25
	Bancroft et al. 1990	Everglades, FL	1987, 89	33	11.5	17.9+
	Frederick 1993	Everglades, FL	1992	102	12.6	≅ 36
	This study	Lake Okeechobee, FL	1989-92	286	4.9	33.3

[a] Three birds followed repeatedly by radio telemetry.

possible exception of Tricolored Herons, I found little evidence that variation in foraging-flight distances was a significant determinant of nest success and productivity at the lake.

The lake region provides a high diversity of foraging opportunities both on and off the lake within a relatively limited area. The close proximity of such an array of choices may generally preclude the need for extensive travel to find foraging opportunities. In addition, it is possible that for most species the relationship between foraging flight energetics and nest success is not a continuous function. Instead, increased flight distances may lead to nest failure only after a certain threshold is reached. For instance, a relatively abrupt transition may occur where the distance to foraging sites becomes so great that the adult birds are no longer able to compensate for extended prey delivery intervals by carrying back larger prey loads. If this is the case, one may not be able to detect an association between flight distances and nest failure rates until a threshold situation is reached (as appeared true in the Everglades cases mentioned above). Moreover, linear trend analyses may not suffice to uncover the relationship.

Variation in flight distances alone apparently did not affect prey delivery rates or the size of prey loads to a degree sufficient to influence productivity levels at the lake (cf. Frederick and Spalding 1994). However, the foraging-flight study highlighted shifts in habitat use among nesting birds that were affected by changing hydrologic conditions, and associated variation in habitat quality may have contributed to differences in annual and colony-specific nest success and productivity. For instance, all species achieved high levels of nest success and productivity during the drought seasons of 1989 and especially 1990 (Table 3-6; Chapters 4 and 5). Habitat selection analyses for the larger non-breeding population (Chapter 2) and the habitat use studies

summarized herein for nesting populations revealed that mixed-submerged habitats--dominated primarily by Hydrilla and Vallisneria--were a strong attractor for foraging birds of all species when the lake stage was low. Furthermore, prey sampling showed that these habitats harbored high densities of small fishes and grass shrimp (McIvor and Smith 1992; Chick and McIvor 1994), and observations of foraging birds indicated generally high foraging success and profitability (unpubl. data). Snowy Egrets and Tricolored Herons were the most inclined to use these habitats, even at higher lake stages. In contrast, White Ibises turned to such habitats only at the height of the drought. At this time, fish and other prey had become highly concentrated in exposed beds of submerged vegetation; this may have provided the opportunity for ibises to switch from a diet dominated by invertebrates to one featuring more fish (sensu Kushlan 1976c, 1979).

Great Egrets were unusual among the species studied in that their flights averaged longer and a higher proportion of their flights ended off the lake in 1990 at the height of the drought than in other years of the study. Several factors may have contributed to the trend. First, Great Egrets are the largest and longest-legged of the four species studied, and therefore often forage in deeper water and on larger prey than the smaller species (Willard 1977; unpubl. data). Accordingly, drought-related declines in surface-water levels may have eliminated foraging habitat suitable for Great Egrets at a faster rate than for other species. Second, Great Egrets showed particularly strong selection for Eleocharis-dominated mixed-prairie habitats and mixed grass habitats at moderate to high stages (Chapter 2), but most of these areas dried out at the height of the drought. Thus, nesting Great Egrets may have been forced at an early stage during the drought to switch to less-preferred habitats. Third, Great Egrets that nested on the lake in 1990 may not have been as able as other species to

take advantage of local enhancement to identify profitable foraging grounds on the lake (Evans 1982; Erwin 1983). Great Egrets nested only at Eagle Bay Island and Clewiston Spit in 1990 (Fig. 3-1), but by May-June 1990 most of the foraging activity on the lake was centered in Fisheating Bay (Fig. 3-1; Chapter 2), beyond the range traveled by most of the nesting birds (Fig. 3-3). In contrast, Snowy Egrets and Tricolored Herons began nesting in 1990 after the spring recession began, and many birds nested on the small spoil islands in Fisheating Bay close to the concentrated foraging activity (Chapter 4).

Thus, although many Great Egrets did forage in various habitats on the lake, a majority of those followed in 1990 (58%) traveled off the lake to dispersed foraging sites in sugar-cane field ditches near Clewiston and in various habitats adjacent to Eagle Bay Island (Fig. 3-3). The sugar cane field ditches and canals, in particular, may have constituted an unnaturally persistent source of flooded habitat during the drought when many natural habitats disappeared. Furthermore, it was during 1990 at the height of the drought that Great Egrets turned most heavily to the unusual foraging strategy of panhandling fish scraps from fishers in residential areas (24% of the birds followed in 1990 versus 5-9% in other years; 41% of the total number of birds followed off-lake in 1990). Nestling regurgitant samples confirmed that many chicks were fed filleted carcasses from black crappie (Pomoxis nigrimaculatus) and other sunfishes taken from the fish-cleaning stations. This food type, along with minnows stolen from bait shop tanks (several of the birds followed landed on bait shop roofs, and several merchants confirmed thievery events), constituted a minimum of 10-12% of the aggregate mass of prey represented in 151 nestling regurgitant samples collected in 1991 (McIvor and Smith 1992). No other species employed the panhandling strategy, and it eliminated the need to find remnant, flooded habitats. Most lakewide measures

of Great Egret nest success and nestling production were highest for the study in 1990 (Chapter 4), so having to rely more on panhandling and other off-lake habitats for foraging was not a disadvantage, just a noteworthy shift in behavior.

In contrast to Great Egrets, Snowy Egrets turned to off-lake habitats only at high lake stages when much of the littoral zone on the lake was too deep for wading and the floating mats in Fisheating Bay had resubmerged or dispersed. The flight distance data alone was not very convincing, but longer flight distances combined with having to rely on off-lake habitats rather than submerged vegetation or mixed-prairie habitats on the lake may have led to increased colony instability and lower nest success in 1992 (Chapter 4). In general, however, it appeared that both Snowy Egrets and especially Tricolored Herons were the most adaptable in terms of being able to maintain fairly consistent levels of nest success and productivity in the face of changing hydrologic and foraging conditions (Chapter 4).

The patterns of habitat use on the lake shown for nesting adults were similar to those demonstrated for the non-breeding population (Chapter 2). Exposed beds of submerged vegetation and outer-fringe habitats were most used at low lake stages. Mixed-prairie habitats, particularly those featuring mixes of Eleocharis, Panicum, and Nymphaea, were most used at moderate lake stages. Upper-elevation transitional mixes featuring grasses and sedges or Polygonum were most used at higher stages. However, the foraging-flight data also indicated that, among all species except perhaps Tricolored Herons, there were always some nesting individuals that chose to forage off the lake. Among Great Egrets and White Ibises, the proportion was always fairly high (28-60% and 24-55%, respectively), but Snowy Egrets regularly traveled off the lake only at high lake stages. The increase in off-lake flights for Snowy Egrets and White Ibises at higher lake stages was consistent with the observation that relatively low

numbers of birds foraged on the lake during the 1991 and 1992 nesting seasons (Chapter 2). Moreover, the number of foraging birds typically increases along Fisheating Creek and in other off-lake areas when the lake stage is high (Zaffke 1984; unpubl. data). Thus, off-lake habitats such as the pocket and slough wetlands interspersed with pasture land and the original Kissimmee River and Fisheating Creek floodplains, should be regarded as important resources for wading birds that nest on or near the lake (cf. Kushlan 1986b). This will be particularly true whenever management action or natural events lead to high lake stages.

The myriad agricultural ditches southwest of the lake also attracted many Great Egrets and Snowy Egrets that nested at Clewiston Spit--Great Egrets primarily during the drought and Snowy Egrets primarily at high lake stages. However, the Great Egret nestlings born at Clewiston Spit in 1990 suffered significantly more than nestlings born at Eagle Bay Island from infections of the nematode parasite Eustrongylides ignotus (Spalding et al. 1994). Although no evidence exists to link infections at Lake Okeechobee to particular habitats, the small oligochaetes that serve as an intermediate host of the parasite appear to prosper in artificially disturbed and nutrient-enriched environments (Spalding et al. 1993; Frederick and Spalding 1994). Examinations of hundreds of small fishes collected on the lake in several habitat types revealed no infected fish--which are the second intermediate host (M. S. Spalding pers. comm.). Both cattle pasture and sugar-cane field ditches more readily fit the description of preferred habitat for the oligochaetes, but the higher incidence of infection at Clewiston Spit suggested that the agricultural field ditches may be a greater source of parasites. This is one area where additional research is greatly needed.

Foraging Sociability

My findings concerning each species' propensity to travel in groups were generally consistent with those of previous studies. Custer and Osborn (1978) found that White Ibises traveled with conspecifics on 17% of the flights they monitored in North Carolina, while only 3-5% of the Snowy Egret, Tricolored Heron, and Great Egret flights involved more than one individual. Ogden (1978b) noted that 29% of the Snowy Egrets and 15% of the Tricolored Herons that departed from a colony in the Everglades did so in groups. Maccarone and Parsons (1988) monitored foraging flights from two colonies off Staten Island, New York and found that 7% of the Snowy Egret flights and 3% of the Great Egret flights involved groups of 2 or 3 birds. Similarly, Erwin (1983) found that only 2-4% of the Snowy Egrets, Tricolored Herons, and Great Egrets departed in groups (2-3 birds) from the colony he studied in North Carolina, and even fewer Snowy Egrets and Tricolored Herons departed in groups from a colony in Virginia (Erwin 1984). Frederick and Collopy (1988) indicated that most of the Great Egrets, Snowy Egrets, and White Ibises they followed from colonies in the Everglades were solitary travelers, but that the ibises did occasionally depart in groups. Thus, the data consistently indicate that White Ibises are the most likely to travel in groups, and that Snowy Egrets are the second most likely to do so. However, in this study many of the birds--particularly Tricolored Herons--that departed in groups did not land in the same location. This suggests that either Bayer's (1982) hypothesis applied--i.e., group departures may be a statistical artifact of grouped arrivals--or that departing in groups may simply have facilitated the location of favorable foraging sites through local enhancement (Evans 1982; Erwin 1983).

The majority of individuals of all species chose to land and begin foraging with or near other wading birds. This fact suggests that most birds relied on local enhancement to identify quality food sources (Krebs 1974; Kushlan 1977; Caldwell 1981; Erwin 1983; Master 1992). Tricolored Herons were the least inclined to join concentrated flocks and tended to land near only smaller aggregations. These results are consistent with previous studies that showed Tricolored Herons tend to remain on the periphery of mixed aggregations (Willard 1977; Kushlan 1978a; Master 1992), are more often found in smaller rather than larger feeding groups (Kushlan 1976b; Erwin 1983) or overall less often in groups (Willard 1977), and do not necessarily benefit in terms of foraging efficiency by associating with aggregations (Master et al. 1993; but see Caldwell 1981). Tricolored Herons often feed solitarily using either very active disturb-and-chase or stealth techniques in open habitats or along the edges of canals (Meyerricks 1962; Jenni 1969; Willard 1977; Rodgers 1983; Kent 1986b; unpubl. data); the efficiency of both techniques is probably less effective near dense aggregations (Kushlan 1978a). In contrast, Snowy Egrets and especially White Ibises usually joined other foraging birds. Snowy Egrets have frequently been cited as the primary attractor and a core species in mixed-species aggregations (Willard 1977; Caldwell 1981; Master 1992), and Jenni (1969) also noted that Snowy Egrets tended to be more social than Tricolored Herons at his study site in central Florida. Master et al. (1993) summarized evidence that suggested Snowy Egrets may actually be obligate aggregation foragers in many cases, because gains in foraging efficiency derived from aggregation foraging may be essential to meet the species' more stringent daily energy requirements (Kent 1986b). However, at Stone Harbor, New Jersey, Snowy Egrets usually were transient, solitarily foragers (Itzkowitz 1984), so the former conclusion may be applicable only under certain conditions. Kushlan (1978b) showed that White Ibises also act as an

attractor in the Everglades (also see Armstrong 1970; Kushlan 1977, 1979), and he discusses in Kushlan (1979) reasons why the foraging strategy of White Ibises dictates that the species nest colonially and feed in aggregations.

Tricolored Herons that sought other individuals as indicators of habitat quality were more likely to choose areas occupied by white-plumaged species than those occupied by only conspecifics, and were most likely to associate with Snowy Egrets rather than White Ibises or Great Egrets. This is consistent with Caldwell's (1981) finding that the species was preferentially attracted to monospecific flocks of model Snowy Egrets as opposed to Great Egret or mixed flocks. However, Great Egrets in this study joined only other Great Egrets 37% of the time, which differs from Caldwell's (1981) findings that the species was preferentially attracted to monospecific flocks of model Snowy Egrets, but never to monospecific flocks of Great Egrets. Nonetheless, during my study Great Egrets that did join non-conspecific individuals joined Snowy Egrets more often than other species. In addition, White Ibises joined flocks that included Snowy Egrets more often than flocks that included White Ibises. I did not gather information about the relative availability of flocks of different composition, so I cannot be sure that the indicated trends reflect preferences, but the results do seem to lend support for the hypothesis that the presence of Snowy Egrets acts as a primary attractor for other species.

Master et al. (1993) found that, although Great Egrets expended less energy when foraging in association with mixed-species aggregations, they did not experience any increase in foraging efficiency (but see Caldwell 1981). In contrast, Wiggins (1991) found that Great Egrets feeding in monospecific groups were less likely to expend energy chasing other birds and achieved higher capture rates and efficiency. The biomass intake rate of solitary birds was equivalent because they usually took larger

fish, but solitary birds were more likely to expend considerable energy defending their feeding territory. He concluded that Great Egrets in Texas probably aggregate only when small fishes are sufficiently concentrated that a high rate of capture yields a similar or greater level of energy gain than fewer captures of larger fish. Erwin (1983) found that Great Egrets were not common in large groups, further indicating that the species often prefers to feed in smaller groups or solitarily, probably because such situations are more amenable to the use of the species usual foraging mode, a slow stalking approach (Willard 1977; Kushlan 1978a; Rodgers 1983). My observations suggested that Great Egrets were most likely to congregate in large, dense groups (up to several hundred individuals) when foraging in relatively open, moderate-depth water in between or on the fringes of beds of submerged vegetation. At these times, the most frequently captured prey were moderate-sized sunfishes and probably small, schooling bass, and Great Blue Herons and Wood Storks were common members of the aggregations (unpubl. data). My observations of many such flocks suggested that the dense concentration of birds elicited chaotic movements among the fishes that rendered them more susceptible to capture. The occurrence of such large groups was probably dependent on the fact that the fish had become concentrated by the severe drought. Otherwise, although I did frequently observe Great Egrets in association with diverse, mixed-species flocks in a variety of situations, a more common sight was scattered individuals spread out in Eleocharis or Panicum-dominated wet-prairie habitats.

Thus, all aspects of the data I have presented confirmed that White Ibises were the most social of the species studied. Hydrologic changes appeared to affect the distances they flew to feed and their choice of foraging habitats more than was true for other species. Ibises also may have been the only species that relied on both

information exchange at the colony and local enhancement to ensure profitable foraging opportunities. However, group departure from colonies is not necessarily a prerequisite for information exchange. Individual birds may take advantage of others simply by following flight lines to productive foraging grounds, without actually joining a departing group (Erwin 1983). My observations suggested that this often occurred at the lake. Furthermore, because ibises typically forage using a tactile, grope-foraging technique, they increase the efficiency of their foraging primarily through habitat selection, rather than by actively searching for concentrations of prey (Kushlan 1979). Flocking and group feeding help insure that foraging time is spent in relatively profitable patches of habitat, and reduces the time spent searching for such patches (Ward and Zahavi 1973; Krebs 1974; Kushlan 1979). In addition, the "beater" effect of foraging around other birds (Kushlan 1979) may increase the chance of random encounters with moving prey, and therefore benefit the tactile-feeding ibises, in particular. Traveling in groups from colonies may simply be one mechanism for insuring that foraging partners are available for interaction, and may also facilitate location of productive habitat via local enhancement (Evans 1982; Erwin 1983). Other data lent further support for this hypothesis: the ibises were the most likely among the species studied to join other foraging birds at foraging sites and to land in the immediate vicinity of other birds as opposed to only nearby, and ibises also tended to join larger flocks than other species.

Snowy Egrets also nearly always joined other foraging birds at foraging sites, suggesting that they too usually took advantage of local enhancement to identify suitable foraging habitat. However, Snowy Egrets did not travel in groups from colonies to foraging sites as often as ibises, suggesting that either they relied less on direct interaction at the colonies or simply were not as dependent on close-association group foraging. Great Egrets were even less apt to follow one another to foraging grounds,

and were also less likely than Snowy Egrets and White Ibises to choose areas already being used by other species. In addition, Great Egrets were unusual in that they took advantage of a unique foraging opportunity, the panhandling technique. Nonetheless, Great Egrets exhibited more social tendencies than Tricolored Herons. Nearly all aspects of Tricolored Heron foraging flight dynamics suggested that, of the species studied, they were the most asocial in their foraging habits and frequently foraged solitarily. It this light, it was interesting to note that Tricolored Herons were the only species for which significant negative correlations between mean flight distances and colony-specific estimates of nest success and productivity were demonstrated.

CHAPTER 4
COLONY DYNAMICS, NEST SUCCESS AND PRODUCTIVITY, AND CAUSES OF NEST FAILURE

Introduction

Much effort has been expended recently in southern Florida to gather information and help regional managers decide how best to accommodate a healthy wildlife fauna in the face of expanding agriculture and human populations. Wading bird ecology has garnered considerable attention, because wading birds are highly visible, dynamic members of the Everglades and southern Florida wetland ecosystems and are regarded as bioindicators of change in hydrological and ecological conditions in wetland ecosystems (e.g., Custer and Osborn 1977; Curry-Lindahl 1978; Hafner and Britton 1983; Bildstein et al. 1990; Kushlan 1986b, 1993; Ogden 1994). Moreover, Florida breeding populations of the majority of ciconiiform species that occur in the state have declined dramatically over the past two decades (Kushlan and White 1977; Ogden 1978a, 1994; Kushlan et al. 1984; Kushlan and Frohring 1986). Most are considered at least "species of special concern" in Florida, if not already listed as threatened or endangered on state or federal registers (Wood 1993). An extensive history of hydrologic manipulation and wetland habitat alteration is the likely cause of the declines (Kushlan 1986a; Walters et al. 1992; Bancroft et al. 1994; Frederick and Spalding 1994; Ogden 1994).

Lake Okeechobee is the third largest freshwater lake in the United States (1,732 km^2 surface area, with 400 km^2 of emergent marsh; Herdendorf 1982). The lake is nearly surrounded by a reinforced earthen dike, and most water flows are controlled by a series of canals, locks, hurricane gates, and pumping stations. However, although

human regulation affects the lake stage to a degree, mostly at high stages, the primary factor controlling water levels in the lake is regional rainfall (Aumen 1994). The South Florida Water Management District, the US Army Corps of Engineers, and the State of Florida Department of Environmental Regulation oversee management of the lake under a multiple-use mandate that attempts to fill needs for flood control, human and agricultural water storage and supply, a multi-million dollar commercial and sport fishing industry, and a variety of recreational and other wildlife-related interests (Aumen 1994). The demands of these diverse interests often conflict. For instance, the nesting activities of several species of wading birds have declined at the lake since 1978 when the stage regulation schedule was increased from 4.4-4.9 m to 4.7-5.3 m NGVD to increase water storage capacity (David 1994a; NGVD = National Geodetic Vertical Datum of 1929, essentially equivalent to height above mean sea level; for convenience, I will henceforth omit the NGVD qualifier). Therefore, it is critical that the decision-makers have accurate and comprehensive information at their disposal concerning the effects of hydrologic and other manipulations on ecosystem integrity.

In Chapter 2, I documented patterns of distribution and abundance and the habitat preferences of foraging wading birds at Lake Okeechobee from 1989-1992, and discussed distributional trends in relation to hydrology and the distribution of vegetation assemblages. In this chapter, I present the results of complimentary studies designed to document the distribution, success, and productivity of the concurrent nesting efforts of six species. A two-year drought cycle that began in late 1988 resulted in low (3.2-3.7 m) and rapidly declining lake levels during the late-winter/spring dry seasons of 1989 and 1990. Much larger populations of foraging birds were attracted to the lake during these periods than in 1991 with moderate (3.7-4.3 m) and more stable water levels, or in 1992 when the lake stage returned to high levels (4.3-5.0 m). Herein, I discuss how hydrodynamic and climatic fluctuations influenced trends in colony establishment, reproductive effort, and nest productivity. I also summarize the documented and

apparent proximate causes of nest failure, and compare the population dynamics of nesting and foraging birds with regards to the management implications.

Methods

Study Species

I studied Great Blue Herons, Great Egrets, Snowy Egrets, Tricolored Herons, Little Blue Herons, and White Ibises. Glossy Ibises, Black-crowned Night Herons, and Green-backed Herons nested in small numbers on the lake, and Cattle Egrets nested in every colony used by other small ardeids, sometimes in large numbers. However, I did not study any of the latter species in detail.

Colony Locations and Composition

I conducted weekly aerial surveys beginning in mid-January each season, 1989-1991, to document the location, composition, and success of all nesting colonies established on the lake and within 15 km of the lake's perimeter. In 1992, I conducted only monthly surveys (a contract-related compromise involving time and budget constraints), and therefore the nesting history was less complete. I often located new colonies during concurrent, bimonthly (monthly in 1992) foraging-dispersion surveys (Chapter 2). I visited every active colony during each survey until all nesting activity ceased. At each visit, I recorded estimates by species of the number of active nests and courting pairs present.

Great Blue Herons and Great Egrets generally nest in the open on top of the vegetation canopy; it is therefore relatively easy to obtain accurate counts of their nests. In contrast, all other species usually nest throughout the vegetation, and aerial nest counts are therefore only rough estimates. White species such as Snowy Egrets and White Ibises are more easily detected and therefore more easily counted, whereas

aerial counts for Little Blue Herons and Tricolored Herons should generally be considered only very rough estimates. However, Little Blue Herons often nested in small monospecific colonies during this study (see Fig. 4-1), and once their white nestlings hatched, it was relatively easy to obtain an accurate count of the number of hatched nests. In addition, each year I repeatedly visited several colonies on the ground to monitor the fate of marked nests (see below), and for these colonies I obtained more accurate nest counts for all species. I also periodically visited other colonies (primarily accessible island colonies; e.g., the SFB, CFB, and CS spoil island colonies shown in Fig. 4-1) to obtain accurate counts of small heron nests. Accordingly, although I can place no estimate of statistical precision on my lakewide nest counts, I believe they accurately reflect interannual trends in reproductive effort and provide a reliable index to the abundance of nesting birds around the lake.

Nest Monitoring

Each year I selected three to four on-lake nesting colonies for intensive studies of nest success and productivity. The sites chosen always included at least two of the largest mixed-species colonies. Additional selections constituted a balance between geographic diversity and adequate species coverage. Great Blue Herons and Little Blue Herons commonly occupied small, isolated, monospecific colonies that I never attempted to visit. Consequently, my estimates of success and productivity for these species are biased toward those individuals that nested in mixed-species colonies, and I obtained very little data for Little Blue Herons in 1991 and none in 1992.

I began checking colonies in early to mid-January each year, with the onset of Great Egret nesting. During the 1989-1991 seasons, I visited each chosen colony repeatedly at 3-8 day intervals, marking new nests whenever time allowed. I continued visits until the majority of nests in a given colony had either failed or most young had fledged and abandoned the site. In 1992, I reduced the frequency of colony visits to

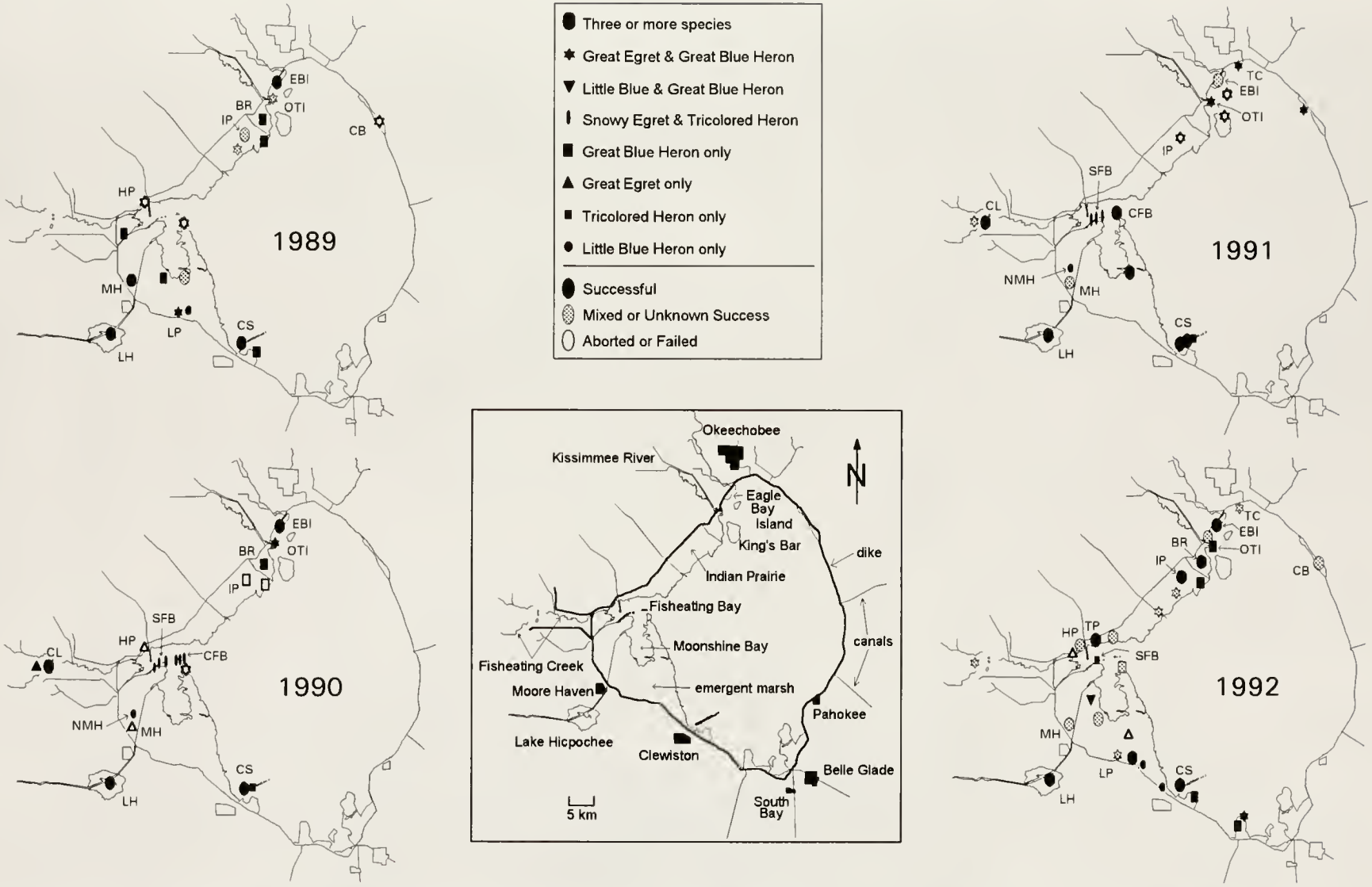


Figure 4-1. Nesting sites involving at least two nests or courting pairs: 1989-1992. Colony name codes are indicated only for those sites mentioned in the text. Symbols denote colony composition and success.

the minimum necessary to allow for confirmation of clutch sizes, hatching success, and nestling survival among a representative sample of nests. In large colonies, I began nest marking excursions at the edge of the colony and continued in a looping pattern into and back out of the center of the concentration of nests to avoid potential edge-effect and nest-density biases. I typically did not mark nests that had nestlings when first discovered, except in the case of Great Blue Herons. This species usually initiated nesting before I began colony checks. If nests with young were present at first visit, I marked a sample (28 of a total of 41 nests followed in 1989; 8 of 63 in 1990; 6 of 67 in 1991; and 7 of 10 in 1992) to obtain a temporally representative estimate of nestling survival.

I was able to identify most nests to species, but the eggs of the three small ardeid species (Snowy Egret, Tricolored Heron, Little Blue Heron) are not readily distinguished (Hammatt 1981). Thus, in mixed-species colonies and without obvious segregation by species, I could not distinguish small ardeid nests that failed to hatch. Little Blue Herons usually remained segregated from other species, except in 1989; therefore, I lumped all small ardied nests to generate an estimate of lakewide hatching success for 1989, but lumped only Snowy Egret and Tricolored Heron nests in generating estimates for 1990-1992.

Nest Success and Productivity

I estimated 1989-1991 annual nest survival probabilities using the Mayfield method (Mayfield 1961, 1975; Hensler and Nichols 1981; Hensler 1985). I also calculated Apparent percent-survived estimates (Johnson and Shaffer 1990) for all years, because in 1992 the extended visitation intervals precluded accurate identification of initiation and hatching dates necessary for calculating Mayfield probabilities. Mayfield survival estimates are advantageous because they can be compared statistically. However, the method assumes constant daily survival

probabilities, and therefore may yield biased estimates if stochastic events lead to the abrupt failure of many nests (Johnson and Shaffer 1990). Calculating both Mayfield and Apparent estimates of nest success therefore also provided a means for identifying biases.

I calculated Mayfield survival probabilities separately for the laying/incubation and nestling periods, because the probability of survival may vary during different stages of the nesting cycle (Black et al. 1984; Custer et al. 1983; Frederick and Collopy 1989a; Mayfield 1961, 1975). I then combined the two period estimates to generate overall probabilities of survival (Hensler 1985), and used Bonferroni multiple comparisons (Neter et al. 1990: 587-589) to assess the significance of interannual differences ($P \leq 0.05$ considered significant; $0.10 \geq P > 0.05$ referred to as marginally significant). I defined a successful nest as one in which at least one egg hatched and one young reached a predefined age threshold.

The incubation period began with the laying of the first egg and the nestling period began with its hatching. I designated incubation period lengths based on a combination of information from the literature (Bent 1926; Palmer 1962; Frederick and Collopy 1989a; Bancroft et al. 1990) and empirical data (Great Blue Herons = 28 days; Great Egrets = 27 days; Snowy Egrets, Tricolored Herons, and Little Blue Herons = 25 days; White Ibises = 21 days).

I set the end of the nestling period for Great Blue Herons equal to 60 days, which corresponded to the approximate age of first flight for the species (Palmer 1962; Pratt 1970). Great Blue Heron nestlings rarely fled their elevated nests when disturbed and therefore could be reliably tracked for extended periods. However, it becomes increasingly difficult to reliably track nestlings of the smaller ardeid species after about 21 days posthatching (Frederick et al. 1993), and White Ibis nestlings after about 14 days posthatching (pers. observ.). These species all nest more or less within the vegetation canopy, and at the indicated stages, the nestlings often remain in the

branches above their nests and are capable of escaping rapidly through the branches when disturbed (McVaugh 1972; Werschkul 1979; Frederick et al. 1993). The degree of tracking difficulty depends on the species involved, the color of the birds, the spacing of nests, and the amount of vegetative cover in the colony (Pratt and Winkler 1985; Frederick et al. 1993; pers. observ.). I found that, with the help of unique color-band combinations to identify individuals, I could reliably track Great Egrets nestlings through to independence in most--but not all--colonies at Lake Okeechobee. However, this was rarely the case for the smaller ardeid and White Ibis species, which typically nested in more concentrated groups and more scattered throughout patches of dense vegetation than the Great Egrets. Thus, for the purpose of calculating lakewide estimates of nest success, I set the endpoint of the nestling period equal to 21 days for Great Egrets, Snowy Egrets, Tricolored Herons, and Little Blue Herons, and to 14 days for White Ibises. The age of first flight for Great Egrets is typically around 42 days, and Wiese (1975) found that fledglings attained independence at 60-70 days of age. Frederick et al. (1993) determined that the age of first flight for Tricolored Herons was 25-30 days, and that most fledglings gained independence at 45-60 days. Thus, the threshold ages represent less than half of the period when young birds are dependent on their parents for food, and associated estimates of success therefore probably overestimate true fledging success. I present data on the possible degree of overestimation in the results section.

I also calculated estimates of annual mean clutch size, mean number of eggs hatched per nest start and per hatched nest, and mean number of nestlings of threshold age produced per nest start and per successful nest (i.e., those that successfully produced at least one young to the threshold age). I conducted Bonferroni t-test multiple comparisons of interannual differences for 1989-1991, but again did not include 1992 data in statistical comparisons. Mean clutch sizes should typically be calculated only from data representing nests that were discovered during and survived

beyond the egg laying stage, because partial clutch losses due occur (Frederick and Collopy 1988). However, I first marked many of the nests I studied after the egg-laying stage had passed. This was particularly true for Great Egrets and Great Blue Herons, because I often first entered the colonies after most pairs had laid eggs. It was frequently the case with Little Blue Heron nests as well, because I often found the species uncommon nests only after noting the persistent presence of adults in certain areas. Therefore, to increase sample sizes, I included all nests that survived beyond the egg-laying stage and that I observed for at least half of the incubation period. I documented partial clutch losses for nests monitored during incubation of 2.8% for Snowy Egrets, 2.8% for Tricolored Herons, 3.1% for Great Blue Herons, 4.5% for Great Egrets, 4.6% for Little Blue Herons, and 6.2% for White Ibises. Thus, partial clutch losses were not common, but restricting the clutch size dataset to nests observed for extended periods reduced the chance of missing the few such events that did occur.

It is important to again acknowledge potential biases associated with using threshold ages, in this case for calculating nestling production statistics. Frederick et al. (1993) estimated that Tricolored Heron nestling mortality per day of exposure after nestlings attained mobility (>14 days of age) was nearly three times higher than during the first 14 days posthatching. Thus, nestling production estimates based on threshold ages may overestimate true fledgling production to a considerable degree, but nonetheless provide an index that is useful for drawing interannual comparisons.

Identifying Causes of Nest Failure

It was usually difficult to identify a specific cause of egg loss, nestling mortality, or nest failure. I assumed that a nest had been abandoned when an entire clutch of cold, intact eggs or a brood of dead, cold, or moribund young remained in or around the nest. The disappearance of entire clutches or broods, or the finding of eggs that had obviously been eaten, implied the involvement of predators, but not necessarily that

their action was the cause of failure. The predator may simply have scavenged the eggs or young following abandonment. Evidence sufficient to confirm a true predation event was available in only a few instances. I assumed that the death of nestlings found in, under, or near nests with live young still present was the result of sibling competition and starvation, unless other information suggested an alternate cause. Dr. Marilyn Spalding of the University of Florida Department of Infectious Diseases conducted necropsy examinations of carcasses recovered in 1989 and 1990, which confirmed a specific cause of death in some cases (e.g., disease and parasites, predator and siblicide trauma, malnutrition).

Results and Discussion

Colony Establishment and Success

Definition of a colony. Nesting wading birds used a total of 37 on-lake and 3 off-lake sites that I designated distinct colony sites (Fig. 4-1) for purposes of calculating annual turnover rates (Erwin et al. 1981). I defined a colony as a group of two or more nests or courting pairs. Three colony sites consisted of series of small spoil islands separated by distances of less than 100 m: Central Fisheating Bay (CFB), one primary and 3 others; South Fisheating Bay (SFB), one primary and up to 8 others; Clewiston Spit (CS), one primary and up to 7 others. The Moore Haven (MH) site consisted of two large and one small--used only in 1991--stands of willow clustered within 200 m of one another. The Eagle Bay Island (EBI) site consisted of a large (3 km^2) expanse of willow and emergent marsh artificially separated from the "mainland" by a canal, and situated immediately adjacent (within 50 m) to the large earthen dike that encircles the lake (Fig. 4-1). In 1991, a mixed-species group shifted from the usual nesting location on the island to a band of willows and Australian Pine (Casuarina equisetifolia) along the dike,

but I did not tally this as a distinct colony. All other colonies were located in discrete stands of vegetation, with inter-colony distances greater than 200 m (Erwin et al. 1981).

Timing of nesting. Great Blue Herons began nesting in early November 1988, mid-to-late December 1989, late November 1991, and mid-January 1991 (fall/winter surveys conducted in 1988, otherwise projected dates of initiation based on the state of nests observed in January). Great Egrets also began the 1989 and 1992 seasons earlier (mid-December) than in 1990 (early January) and 1991 (mid-January). Both species initiated more nests and nested earlier in 1989 and 1992 than in 1990 and 1991. This trend suggested that both species responded favorably when high winter surface-water levels were followed by an early and protracted spring surface-water recession (Fig. 4-2). Great Blue Herons initiated slightly more nests in 1992 than in 1989, possibly indicating a preference for the slower recession rates of 1992. The opposite trend was apparent for Great Egrets (also see Chapter 5). I observed 82 Great Egrets courting on 18 July 1992, and another 12 courting at a new colony site on 16 August. These very late waves of activity coincided with abrupt, but temporary reversals in an otherwise rising surface-water trend (Fig. 4-2). This fact suggested that Great Egrets responded most strongly to receding surface-water levels, rather than to high water levels. The exact correspondence of the peak nesting effort with the onset of a rapid spring surface-water recession in 1990 provided further support for this contention.

White Ibises also exhibited flexibility in initiation dates, having begun to nest as early as mid-March in 1990, and as late as early April in 1991. Moreover, White Ibises initiated late waves of new nests in both 1991 and 1992. The late wave in July 1992 corresponded to the same temporary surface-water recession to which Great Egrets apparently responded (Fig. 4-2). The observation is consistent with Kushlan's (1976c) findings that the species often initiates unseasonable waves of nesting in response to

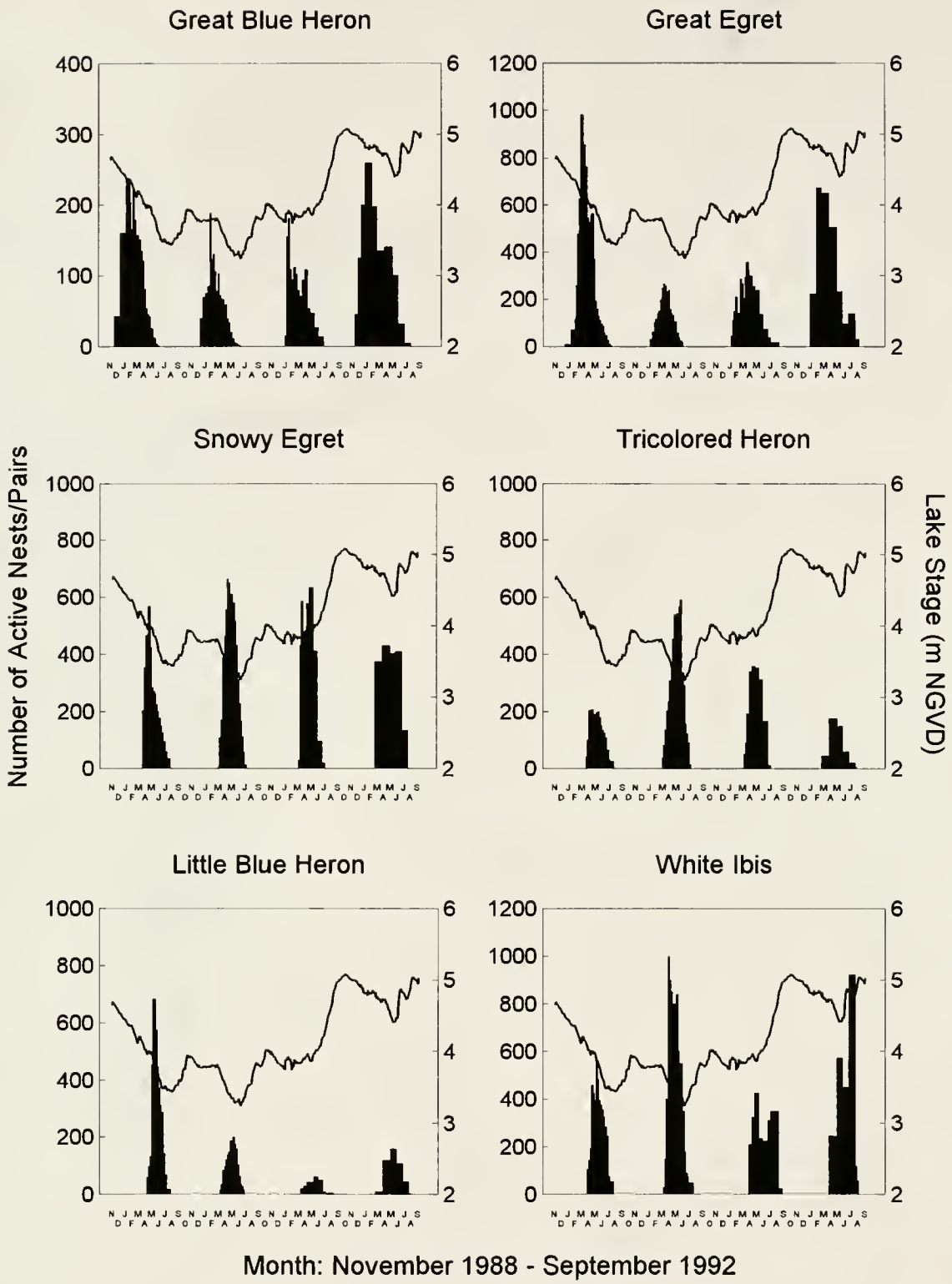


Figure 4-2. On-lake nest counts by species in relation to lake stage: 1989-1992.

unusual surface-water recessions. However, the late wave in 1991 did not correspond to any such hydrologic event, and therefore remained anomalous (Fig. 4-2).

A few Tricolored Herons (<15 pairs) began nesting during the first 10 days of March in 1990 and 1991, but Snowy Egrets and Tricolored Herons typically began nesting within the same two week period each year (10-22 March). Little Blue Herons usually began nesting within a week of the start of Snowy Egret and Tricolored Heron nesting, but did not begin to nest in 1989 until the second week of April. The beginning of Little Blue Heron nesting in 1989, 1990, and 1992 appeared to correspond to the onset of steady surface-water recessions, and the species initiated the lowest number of nests in 1991 when no protracted recession occurred (Fig. 4-2).

Colony composition. Snowy Egrets and White Ibises were the only species that never nested in monospecific colonies. Great Blue and Little Blue herons were the most likely to nest successfully in small, isolated groups (Fig. 4-1). Great Blue Herons nested on 14 occasions in entirely monospecific groups (5 such colonies in 1989, 3 in 1990, 5 in 1992; 26% of 54 group nesting attempts). All such attempts were successful, except for two cases in 1990 (Fig. 4-1). I also frequently observed isolated, single Great Blue Heron nests in 1989 (10) and 1992 (22, including 5 in the Chancy Bay [CB] area marked on Fig. 4-1), and observed single Great Blue Heron nests within mixed-species colonies on four occasions (in 1989 at Harney Pond [HP] and CS; in 1991 on the SFB islands; in 1992 at Twin Palms [TP]). On five more occasions (2 in 1989, 3 in 1992; 9% of the total group attempts), Great Blue Herons initiated small, successful colonies (<15 pairs) and were later joined by Great Egrets (<10 pairs), but only temporarily (no eggs laid). Moreover, in 15 of the remaining cases (28% of the total group attempts), Great Egrets were the only other species to nest in the colony. Small groups of Great Egrets (5-20 pairs) began courting alone on four occasions (2 in 1990, 2 in 1992; Fig. 4-1), but abandoned each effort before laying eggs. Little Blue Herons initiated isolated nesting attempts--joined later by only Cattle Egrets--on five

occasions (one each year 1989-1991, two in 1992; Fig. 4-1) and nested with only six pairs of Great Blue Herons on another occasion in 1992 (6 of 33 or 18% of the total attempts). In mixed-species colonies, it appeared that Tricolored Herons were the least inclined to aggregate in conspecific groups, and scattered pairs nested successfully on the SFB islands in 1992. However, Tricolored Herons did aggregate and nest successfully in monospecific groups on several of the smaller islands at the CS site in 1990 and 1991 (Fig. 4-1).

Colony distribution. At the height of the drought in 1990 (lake stage < 3.7 m; Fig. 4-2), and to a lesser degree in 1991 with only moderate lake stages (3.7-4.3 m), interior-marsh colony sites were mostly abandoned in favor of island sites still surrounded by water. Interior-marsh colonies included those in the Moore Haven (MH and NMH), Liberty Point (e.g., LP), and Indian Prairie (e.g., IP and BR) areas and those around Moonshine Bay (Fig. 4-1). Island colonies included EBI and Okee-Tantie Island (OTI), and the CS, SFB, and CFB spoil island sites (Fig. 4-1). Variation in interannual colony-site turnover rates (Erwin et al. 1981) reflected the shift in distribution; turnover was higher between 1989 and 1990, 1989 and 1991, 1990 and 1992, and 1991 and 1992 than between 1989 and 1992 or 1990 and 1991 (Table 4-1). In addition, although the EBI and CS sites attracted moderate to large, mixed-species groups each year, the number of nests initiated at both colonies increased substantially from 1989 to 1990 as the drought progressed (Table 4-2; Great and Little Blue Herons at EBI the only exceptions to the trend). In many cases, particularly at CS, the number of nests remained high in 1991. Then in 1992 with the return of high water (lake stage above 4.3 m), nest numbers at both sites were again generally reduced to low levels (again two exceptions, White Ibis at EBI and Great Egrets at CS), and the number of species that used the CS site dropped from five to three (Table 4-2). Furthermore, the 1990/91 expansion at CS involved a substantial overflow of small ardeids (165 Snowy Egret, 243 Tricolored Heron, and 65 Little Blue Heron nests in 1990, along with many Cattle

Table 4-1 Interannual nesting colony turnover rates: 1989-1992.

Year Comparisons	Total Number of Colonies Used Each Year	Number of Colonies Exclusive to Each Year	Turnover Rate[a]
1989 , 1992	18 , 30	3 , 15	0.333
1990 , 1991	15 , 16	4 , 5	0.290
1989 , 1990	18 , 15	8 , 5	0.389
1989 , 1991	18 , 16	12 , 10	0.646
1990 , 1992	15 , 30	3 , 18	0.400
1991 , 1992	16 , 30	7 , 21	0.569
Average Annual Turnover Rate			0.438

[a] Turnover rate (yr^{-1}) = $(S_1/N_1 + S_2/N_2) / 2$, where S_1 and S_2 equal the number of sites exclusive to each year, and N_1 and N_2 equal the total number of sites occupied each year (Erwin et al. 1981)

Egrets) onto several of the smaller, previously inundated islands in the chain. Similarly, none of the small Fisheating Bay islands were used in 1989, and only a few scattered Tricolored Herons and Cattle Egrets nested on the SFB islands in 1992 (Fig. 4-1, Table 4-2). As was true at the smaller CS islands, stands of Phragmites that emerged and supported nests on the CFB islands all but disappeared at higher lake stages. The SFB islands supported persistent and more supportive willow and wax myrtle (Myrica cerifera), but also failed to attract more than a few pairs outside the 1990/91 seasons. David (1994a) documented the same trend over the 12 years prior to this study (with the CFB and SFB islands collectively termed the "Rock Islands" site). The two primary off-lake colonies at Lake Hicpochee (LH) and Cowpen Lake (CL)--both islands in the middle of small lakes--also expanded greatly in size and complexity in 1990 and 1991 (Fig. 4-1, Table 4-2).

Table 4-2 Comparison of annual peak nest and species counts at primary interior-marsh and island colony sites (see Fig. 4-1 for colony locations).

	Interior-Marsh Colony Sites			
Year	BR	IP	MH	LP
1989	29 (1)[a]	295 (5)	1556 (6)	142 (2)
1990	45[b] (1)	3[b] (1)	12[b] (1)	0
1991	0	8[b] (2)	330 (6)	0
1992	147 (4)	331	847 (6)	15 (2)

	Island Colony Sites					
	EBI	CS	SFB	CFB	CL	LH
1989	834 (6)	153 (5)	0	0	0	262 (5)
1990	1960 (6)	771 (5)	217 (2)	157 (2)	590 (4)	500 (5)
1991	1206 (6)	488 (5)	203 (3)	228 (3)	130 (4)	265 (4)
1992	1148 (6)	141 (3)	5 (1)	0	0	180 (4)

[a] Number of active nests or courting pairs (number of species).

[b] All or mostly failed or aborted.

In contrast to the above cases, the interior-marsh MH colony attracted a large and successful mixed-species assemblage in 1989, but was essentially unused in 1990 when most of the surrounding marsh had dried (12 Great Egrets were seen courting, but did not build nests; Fig. 4-1, Table 4-2). In 1991, the MH colony was occupied, but by only small numbers of successful small ardeids, Great Blue Herons and White Ibises, and moderate numbers of mostly unsuccessful Great Egrets (Table 4-2). In 1992, with the return of high water, a large, generally successful (except Great Egrets) group of all species again used the site. Similarly, the IP site was occupied in 1989 by a large group of Great Blue Herons and Great Egrets, and later by small numbers of Little Blue Herons, Snowy Egrets and Tricolored Herons, and several hundred Cattle

Egrets (Table 4-2). However, by the middle of the nesting season most of the surrounding marsh had dried, and all except the Great Blue Herons eventually failed in their nesting efforts at this colony. In 1990 and 1991, only very small groups of Great Blue Herons and Great Egrets courted at the site, without building nests. Then with the return and persistence of high surface-water levels in 1992, a large mixed-species group nested successfully at the site. The only interior colonies that fledged young in 1990 were the perennial Buckhead Ridge (BR) Great Blue Heron colony and the North Moore Haven (NMH) colony occupied by a small group of Little Blue Herons (10-15 nests). However, only 8 of 45 pairs (18%) succeeded in producing young at the BR colony in 1990, as compared with 16 of 29 (55%) in 1989 and most of 37 nests in 1992, and the colony was not used in 1991.

Two factors may have influenced this drought-related shift in colony locations. Birds may instinctively select sites surrounded by water to reduce the threat of invasion by terrestrial predators (Jenni 1969; Frederick and Collopy 1989b; Kelly et al. 1993); however, in this case the shift to on-lake island sites--particularly SFB and CFB--might have occurred in part because the chosen islands were located nearer to productive foraging grounds around exposed beds of submerged vegetation (Chapter 2). The fact that nest numbers and species diversity increased at both on- and off-lake island sites--the latter not located any closer to productive foraging grounds than the abandoned marsh sites--suggested that avoidance of predators might have been the more important concern. The history of events at the 1989 IP colony provided further support for this contention (see Causes of Failure section below).

Reproductive effort and colony success. The 1989/90 drought cycle rendered several small spoil islands at SFB, CFB, and CS available to nesting birds, but the high lake levels of 1992 clearly provided a greater variety of potential colony sites (Fig. 4-1). However, a higher number of colony initiations did not necessarily translate to higher reproductive effort or success. All species except White Ibises succeeded in fledging

young from a greater number of colonies in 1992, but the percentage of failed (eggs laid), aborted (no eggs laid), or uncertain-fate (small numbers of nests, difficult to ascertain success from the air) colony attempts was higher among all species except Great Blue Herons (Table 4-3). Moreover, only Great Blue Herons and Great Egrets initiated more nests in 1989 and 1992 when the season began with high lake levels (Fig. 4-2). Little Blue Herons also initiated more nests in 1989, but the lake stage at the time of initiation was similar in 1991 and higher in 1992 when nest numbers were very low. This suggested that variation in long-term antecedent hydrologic conditions might have been important to the success of Little Blue Heron nesting (discussed further below).

The number of nests initiated on the lake by Snowy Egrets remained relatively consistent from 1989 through 1991, then dropped in 1992 (Fig. 4-2); however, if the number of nests initiated at the LH and CL off-lake colonies (Fig. 4-1) are included (peak numbers 55 in 1989, 405 in 1990, 140 in 1991, and 60 in 1992), the 1990 total rises well above the counts for other years and the margin of difference between 1989 and 1991 increases in favor of 1991. Off-lake totals for other species were comparatively insignificant as far as overall trends were concerned. Tricolored Heron nest numbers were low in both 1989 and 1992, and were clearly highest in 1990 (Fig. 4-2). White Ibis nest numbers were low in 1989 and 1991, highest in 1990, and high in 1992 (Fig. 4-2); however, the high peak in 1992 is misleading in that it occurred very late in the season and most if not all of these nests failed as heavy summer rains began. Individual-nest productivity statistics (presented in next section) further confirmed that Little Blue Herons fared best in 1989 and second best in 1990, and that Great Blue Herons probably did as well in 1992 as in 1990. However, productivity statistics showed that all other species did best in 1990 when the lowest number of colonies was active.

Table 4-3. Proportion of successful, failed, aborted (no eggs laid), and uncertain-fate nesting colony initiations by species and year.

Species	Year	# Colonies	% Succeeded	% Failed	% Aborted	% Uncertain
Great	1989	15	66	7	0	27
Blue	1990	6	50	33	17	0
Heron	1991	14	50	29	21	0
	1992	22	86	0	0	14
	Total	57	69	12	7	12
Great	1989	11	45	28	27	0
Egret	1990	8	62	0	38	0
	1991	15	53	27	13	7
	1992	19	58	16	26	0
	Total	53	55	19	24	2
Snowy	1989	6	83	17	0	0
Egret	1990	6	100	0	0	0
	1991	10	80	0	20	0
	1992	13	61	8	23	8
	Total	35	77	6	14	3
Tricolored	1989	6	83	17	0	0
Heron	1990	6	100	0	0	0
	1991	9	89	0	11	0
	1992	11	82	9	0	9
	Total	32	88	6	3	3
Little	1989	7	86	14	0	0
Blue	1990	5	100	0	0	0
Heron	1991	7	100	0	0	0
	1992	13	69	0	0	31
	Total	32	84	3	0	13
White	1989	4	100	0	0	0
Ibis	1990	3	100	0	0	0
	1991	3	33	33	33	0
	1992	3	67	0	33	0
	Total	13	77	8	15	0

Individual-Nest Success and Productivity

Great Blue Herons. I followed the fate of 41 nests at the EBI colony in 1989 (17% of the estimated lakewide peak total; see Table 4-4), 63 at EBI in 1990 (33%), 29 at EBI and 37 at OTI in 1991 (36%), and 5 at EBI and 5 at IP in 1992 (4%). The lakewide Mayfield probability of hatching for Great Blue Herons was 63% in 1989, 76% in 1990, and 29% in 1991 (Table 4-4). Only the difference between 1990 and 1991 was statistically significant ($P \leq 0.05$). A small hatching-period sample size of only 13 nests in 1989 (the other 28 already had young when first discovered) precluded a significant finding for 1989 versus 1991. Moreover, the data for 1989 might have underestimated true success, because the few nests on which the estimate was based were initiated relatively late in the season (i.e., in late December or January, rather than November). Other analyses have revealed that date-of-initiation and the probability of hatching failure are positively correlated (Chapter 5). I also followed only 10 nests in 1992, and only four of these had eggs when discovered. One of the latter nests failed to hatch, which would have yielded a Mayfield estimate of hatching success near 75%. In contrast, the Apparent estimates of success--including all nests in the calculations--were 93% in 1989 and 90% in 1992, which both rated higher than the Apparent estimate for 1990 of 87% (Table 4-4). The higher, Apparent estimates were more consistent with the higher number of nest initiations in 1989 and 1992 (Fig. 4-2). There was also a large discrepancy in the Mayfield and Apparent estimates of 1991 hatching success (29% versus 50%). This was a result of bias introduced in the Mayfield estimate because a large-scale, synchronous abandonment at the EBI site (discussed further below) resulted in a fluctuating mortality rate (Johnson and Shaffer 1990). Nonetheless, trends in nest numbers and observations of failure at other colonies suggested that the Mayfield estimate more accurately represented the history of events.

Table 4-4. Peak-total and marked nest counts, and nest success and productivity statistics by year for Great Blue Herons.

NEST COUNTS	1989	1990	1991	1992
Peak number of nests on-lake	238	189	181	255
Peak number of nests off-lake	0	0	11	11
Number of colonies monitored	1	1	2	2
Total nests monitored	41	63	66	10
Nests monitored - laying/incubation	13	55	60	10
Nests monitored - nestling period	38	55	33	9
Nests w/ 60d nestlings	22	43	29	6-8
MAYFIELD SUCCESS				
Laying/incubation	0.630 ± 0.1682 ab[a]	0.764 ± 0.0728 a	0.291 ± 0.0625 b	
Nestling	0.467 ± 0.0889 b	0.772 ± 0.0577 a	0.862 ± 0.0638 a	
Combined	0.294 ± 0.0976 b	0.590 ± 0.0715 a	0.251 ± 0.0572 b	
APPARENT SUCCESS				
% Nest starts hatched	92.7	87.3	50.0	90.0
% Hatched nests w/ 60d nestlings	57.9	78.2	87.9	66.7-88.9
% Nest starts w/ 60d nestlings	53.7	68.3	43.9	60.0-80.0
PRODUCTION STATISTICS				
Clutch size	3.0 ± 0.44 b[b]	3.5 ± 0.59 a	3.1 ± 0.95 b	3.10
Eggs hatched per nest start	2.1 ± 0.86 b	2.7 ± 1.30 a	1.3 ± 1.50 c	2.1-2.3
Eggs hatched per hatched nest	2.2 ± 0.66 b	3.0 ± 0.87 a	2.6 ± 1.03 ab	2.3-2.6
60d nestlings per nest start	0.8 ± 0.83 b	1.3 ± 1.10 a	0.7 ± 0.91 b	1.0-1.4
60d nestlings per successful nest	1.5 ± 0.51 b	1.9 ± 0.76 a	1.6 ± 0.68 ab	1.7-1.8

[a] Annual survival probabilities with the same letter cannot be separated using Bonferroni normal *z*-tests with $\alpha = 0.05$. Hensler (1985) provides the formula for calculating *z* values. No tests for 1992.

[b] Production estimates with the same letter cannot be separated using Bonferroni *t*-tests with $\alpha = 0.05$. No tests for 1992.

The Mayfield probability that a hatched nest fledged at least one young was 47% in 1989, 77% in 1990, and 86% in 1991, with the estimate for 1989 significantly lower than for both 1990 and 1991 (Table 4-4). Thus, the combination of moderate hatching success and low fledging success in 1989, and the combination of very low hatching success but high fledging success in 1991 both resulted in significantly lower overall success compared to 1990 (29% in 1989, 59% in 1990, 25% in 1991). According to Apparent estimates of overall success, 1991 (44%) ranked further behind 1989 (54%) than was indicated by the Mayfield estimates, and both 1989 and 1991 rated lower than 1990 (68%), but less so than indicated by the Mayfield estimates. In 1992, at least six and possibly eight of the nine hatched nests fledged at least one young (67-89%). The Apparent estimate of overall success therefore ranged from 60-80%, comparable to the estimate for 1990.

All egg and nestling production statistics confirmed that 1990 was the most productive year for those Great Blue Herons that chose to nest, and that 1992 was at least moderately productive (Table 4-4). All aspects of production--clutch size, eggs hatched per nest start and per hatched nest, and young fledged per nest start and per successful nest--were significantly greater in 1990 compared to 1989. Mean clutch size was insignificantly higher in 1991 (3.1) compared to 1989 (3.0), and significantly lower in 1991 compared to 1990 (3.48). However, hatched-egg production per nest start was significantly lower in 1991 (1.3) than in both 1989 (2.1) and 1990 (2.7), because a late-winter cold front resulted in the failure of many nests that had not yet hatched eggs (see Causes of Failure section below). For the same reason, the production of fledged young per nest start was insignificantly lower in 1991 (0.7) than in 1989 (0.8), and significantly lower than in 1990 (1.3). In contrast, the number of eggs hatched and young fledged per successful nest in 1991 was intermediate between 1989 and 1990, with no differences significant. The maximum estimates for 1992 production parameters fell below the estimates for 1990, except in the case of fledged young per

nest start, and in all cases the minimum estimates for 1992 exceeded those for both 1989 and 1991. Moreover, additional evidence gathered during aerial surveys (many more colonies, more nests, and little evidence of abandonment) further confirmed that Great Blue Herons did well in 1992.

Great Egrets. I followed a combined total of 99 nests at three colonies in 1989 (50 at EBI, 28 at MH, 21 at HP; 10% of the estimated peak on-lake total; see Table 4-5), 171 nests at two colonies in 1990 (88 at EBI, 83 at CS; 65% of the total), 279 nests at four colonies in 1991 (100 at EBI, 40 at OTI, 125 at CS, 14 at CFB; 61% of the total), and 121 nests at three colonies in 1992 (46 at EBI, 28 at IP, 47 at MH; 19% of the total).

The Mayfield probability of nest survival to hatching was significantly lower in 1989 (10%) than in 1991 (34%), and was significantly lower in 1991 than in 1990 (65%) (Table 4-5). The probability that a hatched nest produced at least one 21-day nestling was insignificantly lower in 1989 (67%) than in 1990 (82%), and the estimate for 1991 (91%) was significantly higher than in 1989 and marginally higher than in 1990 (but recall the potential bias mentioned above). The combination of very low hatching success and only moderate nestling-period success resulted in an even lower overall probability of survival in 1989 (6%; significantly lower than in 1990 and 1991). Similarly, low hatching success in 1991 resulted in significantly lower overall success (31%) than in 1990 (61%), despite slightly higher nestling-period success in 1991.

There was a large discrepancy between the Mayfield (10%) and Apparent (55%) estimates of hatching success for 1989 (Table 4-5), a difference that arose because of the coincidence of my first colony visits with a strong late-winter cold front that resulted in temporarily high failure rates (discussed further below). Johnson and Shaffer (1990) emphasized that the Mayfield estimator performs poorly if synchronous abandonments occur. The bias might have been further exaggerated in this case, because the observation periods for some nests that failed were very short and the Mayfield method

Table 4-5. Peak-total and marked nest counts, and nest success and productivity statistics by year for Great Egrets.

NEST COUNTS	1989	1990	1991	1992
Peak number of nests on-lake	982	265	459	649
Peak number of nests off-lake	74	145	185	134
Number of colonies monitored	3	2	4	3
Total nests monitored	99	171	279	121
Nests monitored - laying/incubation	63	168	278	121
Nests monitored - nestling period	54	126	127	84-85
Nests w/ 21d nestlings	40	104	116	53-75
MAYFIELD SUCCESS				
Laying/incubation	0.100 ± 0.0343 c[a]	0.652 ± 0.0416 a	0.343 ± 0.0298 b	
Nestling	0.675 ± 0.0709 b	0.816 ± 0.0353 (a)b	0.913 ± 0.0252 a	
Combined	0.067 ± 0.0243 c	0.532 ± 0.0410 a	0.313 ± 0.0285 b	
APPARENT SUCCESS				
% Nest starts hatched	54.6	73.7	45.5	69.4-70.3
% Hatched nests w/ 21d nestlings	74.1	82.5	91.3	63.1-88.2
% Nest starts w/ 21d nestlings	40.4	60.8	41.6	43.8-62.0
PRODUCTION STATISTICS				
Clutch size	2.7 ± 0.47 b[b]	3.1 ± 0.55 a	2.8 ± 0.54 b	2.9
Eggs hatched/nest start	1.4 ± 1.36 b	2.0 ± 1.39 a	1.2 ± 1.34 b	1.6-1.8
Eggs hatched/hatched nest	2.6 ± 0.60 a	2.7 ± 0.84 a	2.5 ± 0.66 a	2.4-2.6
21d nestlings/nest start	0.9 ± 1.14 b	1.4 ± 1.23 a	0.8 ± 1.08 b	0.6-1.2
21d nestlings/successful nest	2.2 ± 0.59 ab	2.3 ± 0.69 a	2.0 ± 0.69 b	0.9-1.6

[a] Annual survival probabilities with the same letter cannot be separated using Bonferroni normal *z*-tests with $\alpha = 0.05$. Letters in parentheses indicate marginally significant differences separable at $\alpha = 0.10$. Hensler (1985) provides the formula for calculating *z* values. No tests for 1992.

[b] Production estimates with the same letter cannot be separated using Bonferroni *t*-tests with $\alpha = 0.05$. No tests for 1992.

prorates estimates of success based on the time each nest has been observed (Mayfield 1961, 1975). Nonetheless, as with Great Blue Herons in 1991, other evidence gathered during aerial surveys of colonies not visited on foot confirmed that many more incubated nests failed during the same period. Thus, the low estimate of hatching success seemed appropriate (additional details discussed below).

The Mayfield estimate of hatching success for 1991 was also lower than the Apparent estimate (34% versus 45%; Table 4-5), and a similar bias may have applied. Another large-scale synchronous abandonment occurred at EBI (the same event mentioned above for Great Blue Herons and discussed further below); but the discrepancy was less pronounced because the average observation period was longer. The Mayfield estimates ranked 1991 as a better year overall than 1989, but a comparison of Apparent estimates revealed little difference between 1989 and 1991 (40 and 42%, respectively). In contrast, both the Mayfield and Apparent estimates of hatching and nestling-period success were at least moderately high in 1990 (65% and 74% for hatching; 82-83% for nestling), and both estimates of overall success (Mayfield 53%, Apparent 61%) were higher than in 1989 and 1991 (Table 4-5). Subsequent colony surveys suggested that many of the birds that failed early in 1991 renested. I followed 43 of 60 nests built a month later on EBI and overall Mayfield success was 56%, which exceeded the estimate for 1990. There was also a group of about 35 pairs that nested successfully with 10 pairs of Great Blue Herons on the Taylor Creek (TC) island nearby (Fig. 4-1). However, only 10 of 50 pairs that laid eggs at OTI over the following 2-3 weeks succeeded in fledging young (40 nests monitored; 10% overall Mayfield success; most failed with eggs). Similarly, a group of 24 pairs, along with 26 pairs of Great Blue Herons, appeared to shift to the EBI dike location, but all eventually failed. Thus, renesting probably occurred, but overall did not yield a higher level of nest success.

The Apparent estimate of hatching success for 1992 was 69-70% (one nest of uncertain hatching fate), which ranked high in comparison to 1989 and 1991, and only slightly lower than for 1990 (Table 4-5). However, the estimate of nestling-period success for 1992 was much less precise (63 to 89%; 53 of 84 hatched nests definitely succeeded, 22 uncertain). The estimate of overall success for 1992 therefore ranged from 44 to 63%, which at the high end barely exceeded the estimate for 1990 (61%), and at the low end barely exceeded the estimates for 1989 and 1991 (40 and 42%). Thus, 1992 was at least a moderately successful year for Great Egrets in terms of whole-nest survival, as was true for Great Blue Herons.

Each year 1989-1991, I confirmed that between 0.8-5.6% (2.6% overall) of the hatched Great Egret nests failed at >21 days posthatching (Table 4-6). However, between 11.9-24.4% (19.2% overall) of the hatched nests produced one or more nestlings aged >21 days, but I was unable to verify whether any of the associated nestlings fledged (reached 42 days of age) or all perished. However, the overall number of fledglings and a general lack of carcasses in the colonies suggested that whole-nest failures were uncommon late in the nesting cycle. Carcasses could have been consumed by scavengers, but few of the potential scavengers would have been able to carry off a large Great Egret nestling, and most would not have consumed the entire carcass, bones and feathers included. The only possible exception was alligators, but they were not common in the immediate vicinity of nests except at the 1989 Moore Haven and Eagle Bay Island colonies. Carcasses of the small, dark wading bird species may have been difficult to spot, especially in thick vegetation (Frederick et al. 1993), but it would have been difficult to miss large, white Great Egret carcasses, particularly given that the understory vegetation in most colonies was reasonably sparse. Accordingly, although the estimates of 21-day nestling-period success may overestimate fledging success by as much as 27%, I believe that a difference of 3-5%, perhaps as high as 10%, is more likely. Furthermore, only one

Table 4-6. Hatched-nest survival in relation to nestling age: examination of bias associated with using threshold ages to estimate nest success. (Numbers in parentheses indicate confirmed post-threshold nest failures.)

GREAT EGRET

	1989	1990	1991	Total	% Nests
Nests failed at <21 days	14	22	11	47	15.3
Active nests last confirmed at:					
21-42 days	(3) 13	(1) 15	(4) 31	(8) 59	(2.6) 19.2
42-60 days	20	48	41	109	35.5
>60 days	4	40	40	84	27.4
Total	54	126	127	307	

SNOWY EGRET

	1989	1990	1991	Total	% Nests
Nests failed at <21 days	19	12	17	48	20.0
Active nests last confirmed at:					
21-28 days	(1) 20	(1) 49	41	(2) 110	(0.8) 45.8
28-35 days	(1) 4	(1) 13	(2) 12	(4) 29	(1.7) 12.1
35-45 days	8	3	11	22	9.2
>45 days	6	15	4	25	10.4
Total	59	94	87	240	

TRICOLORED HERON

	1989	1990	1991	Total	% Nests
Failed at <21 days	2	11	10	23	15.6
Active nests last confirmed at:					
21-28 days	3	12	(1) 10	(1) 25	(0.7) 17.0
28-35 days	0	5	14	19	12.9
35-45 days	2	8	23	33	22.4
>45 days	12	20	14	46	31.3
Total	19	56	72	147	

LITTLE BLUE HERON

	1989	1990	1991	Total	% Nests
Failed at <21 days	14	8	1	23	29.9
Active nests last confirmed at:					
21-28 days	2	13	0	15	19.5
28-35 days	2	(1) 7	2	(1) 11	(1.3) 14.3
35-45 days	5	3	1	9	11.7
>45 days	7	10	1	18	23.4
Total	30	42	5	77	

WHITE IBIS

	1989	1990	1991	Total	% Nests
Failed at <14 days	4	11	20	35	24.5
Active nests last confirmed at:					
14-28 days	(2) 4	36	(3) 33	(5) 73	(3.5) 51.0
28-35 days	5	2	2	9	6.3
35-45 days	3	2	0	5	3.5
>45 days	11	5	0	16	11.2
Total	29	56	58	143	

possible bias with regards to interannual comparisons emerged. The pre-threshold statistics suggested that fewer hatched nests succeeded in producing 21-day nestlings in 1990 than in 1991 (Table 4-5), whereas the post-threshold statistics suggest that a higher proportion of the 1990 nests produced at least one nestling capable of flight (Table 4-6). The latter is more consistent with trends in per nest production discussed below.

The hatched-egg and 21-day nestling production statistics indicated that Great Egrets fared best in 1990, second best in 1989, and generally worst in 1992 (Table 4-5). Thus, the production statistics most closely matched trends shown for Apparent estimators of nest success, particularly with regards to comparisons of 1989 versus 1991. Estimates of mean clutch size (3.1) and hatched-egg and 21-day nestling production per nest start (2.0 and 1.4, respectively) were significantly higher in 1990 than in 1989 (2.7, 1.4, 0.9) and 1991 (2.8, 1.2, 0.8). The mean number of eggs hatched and 21-day nestlings produced in successful nests were also higher in 1990 (2.7 versus 2.6 in 1989 and 2.5 in 1991, and 2.3 versus 2.2 and 2.0 for nestling production), but the differences were statistically insignificant except for 1990 versus 1991 nestling production. These facts suggested that, although stochastic events such as late-winter storms led to high rates of whole-nest failure early in 1989 and 1991, the quality of foraging opportunities available to nesting adults remained more consistent from 1989-1991. As with estimates of success, the mean clutch size in 1992 (2.9) ranked moderate in comparison to other years, as did the full range of possible values for eggs hatched per nest start (1.6-1.8). Conversely, the range of values for eggs hatched per hatched nest (2.4-2.6) and for 21-day nestlings produced per nest start (0.6-1.2) ranged from below the lowest estimates for other years to moderate in comparison. Moreover, even the maximum possible estimate of 21-day nestlings produced per successful nest in 1992 (range 1.3-1.9) was lower than for any other year (2.0-2.3). Therefore, although egg production and hatching success might have been

moderate in 1992, the range of possibilities for all estimates of nestling success and production included values lower than for other years. Moreover, the number of 21-day nestlings produced in nests that succeeded in producing at least one such nestling was much lower than in other years. These facts suggested that the quality of foraging conditions for nesting Great Egrets was lowest in 1992.

Estimates of 42-day nestling production per nest start ranged from 0.5-0.8 ± 1.0-1.1 in 1989, 1.1-1.3 ± 1.1 in 1990, and 0.6-0.7 ± 0.9 in 1991. Thus, the 21-day production statistics overestimated fledgling production per nest start for 1989 by 12.5-44.3%, for 1990 by 8.7-18.8%, and for 1991 by 19.3-31.3%. However, the only difference in conclusions is that the range of 42-day statistics (Table 4-6) indicate fledgling production in 1991 was proportionately lower than indicated by the 21-day statistics (Table 4-5).

Snowy Egrets and Tricolored Herons. I monitored 59 confirmed Snowy Egret nests, 14 confirmed Tricolored Heron nests, and 23 unidentified small ardeid nests at the MH colony in 1989 (<14% of the estimated peak on-lake total for Snowy Egrets; see Table 4-7). I also followed 5 Tricolored Heron nests and 22 unidentified nests at the EBI colony (combined-total, probable maximum 16% of the peak total for Tricolored Herons; see Table 4-8). Some of the unidentified nests at the MH colony and most of the unidentified nests at the EBI colony probably belonged to Little Blue Herons. In 1990, I followed 114 Snowy Egret, 56 Tricolored Heron, and 54 unidentified Snowy Egret/Tricolored Heron nests in three colonies (EBI, CS, and SFB; maximum 25% of total for Snowy Egrets, 19% for Tricolored Herons; see Tables 4-7 and 4-8, respectively). In 1991, I followed 87 Snowy Egret, 88 Tricolored Heron, and 67 unidentified Snowy Egret/Tricolored Heron nests in three colonies (EBI, CS, CFB; maximum 26% of total for Snowy Egrets, 43% for Tricolored Herons). In 1992, I followed 29 Snowy Egret nests in three colonies (EBI, IP, MH; 7% of peak total) and 9 Tricolored Heron nests in two colonies (EBI, MH; 6% of peak total).

Table 4-7. Peak-total and marked nest counts, and nest success and productivity statistics by year for Snowy Egrets.

NEST COUNTS	1989	1990	1991	1992
Peak number of nests on-lake	570	664	586	430
Peak number of nests off-lake	55	405	140	60
Number of colonies monitored	1	3	3	3
Nests monitored - laying/incubation[a]	106	169	184	29
Nests monitored - nestling period	59	94	87	26
Nests w/ 21d nestlings	40	82	70	10-19
MAYFIELD SUCCESS				
Laying/incubation[a]	0.680 ± 0.0547 a[b]	0.663 ± 0.0415 a	0.643 ± 0.0386 a	
Nestling	0.782 ± 0.0441 b	0.912 ± 0.0242 a	0.798 ± 0.0436 (a)b	
Combined	0.532 ± 0.0523 a	0.605 ± 0.0411 a	0.513 ± 0.0417 a	
APPARENT SUCCESS				
% Nest starts hatched	78.7	77.8	72.9	89.7
% Hatched nests w/ 21d nestlings	67.8	87.2	80.5	38.5-73.1
% Nest starts w/ 21d nestlings	53.4	67.9	58.6	34.5-65.5
PRODUCTION STATISTICS				
Clutch size	3.5 ± 0.50 a[c]	3.3 ± 0.56 b	3.3 ± 0.61 b	3.40
Eggs hatched/nest start	2.4 ± 1.39 a	2.2 ± 1.36 ab	2.0 ± 1.42 (b)	2.5-2.9
Eggs hatched/hatched nest	3.2 ± 0.67 a	2.8 ± 0.83 b	2.9 ± 0.86 (a)b	2.8-3.2
21d nestlings/hatched nest	1.3 ± 1.10 (b)	1.7 ± 1.11 a	1.5 ± 1.05 ab	0.8-1.5
21d nestlings/successful nest	2.0 ± 0.63 a	2.1 ± 0.83 a	1.9 ± 0.77 a	2.0-2.1

[a] Combined-species calculations except in 1992: Snowy Egret, Tricolored Herons, and Little Blue Herons in 1989; Snowy Egrets and Tricolored Herons in 1990 and 1991.

[b] Annual survival probabilities with the same letter cannot be separated using Bonferroni normal *z*-tests with $\alpha = 0.05$. Letters in parentheses indicate marginally significant differences separable at $\alpha = 0.10$. Hensler (1985) provides the formula for calculating *z* values. No tests for 1992.

[c] Production estimates with the same letter cannot be separated using Bonferroni *t*-tests with $\alpha = 0.05$. Letters in parentheses indicate marginally significant differences separable at $\alpha = 0.10$. No tests for 1992.

Table 4-8. Peak-total and marked nest counts, and nest success and productivity statistics by year for Tricolored Herons.

NEST COUNTS	1989	1990	1991	1992
Peak number of nests on-lake	207	590	359	144
Peak number of nests off-lake	18	85	28	15
Number of colonies monitored	2	3	3	2
Nests monitored - laying/incubation[a]	154	169	217	9
Nests monitored - nestling period	19	56	72	9
Nests w/ 21d nestlings	17	45	62	5-6
MAYFIELD SUCCESS				
Laying/incubation[a]	0.599 ± 0.0463 a[b]	0.663 ± 0.0415 a	0.612 ± 0.0359 a	
Nestling	0.894 ± 0.0708 a	0.860 ± 0.0392 a	0.858 ± 0.0416 a	
Combined	0.536 ± 0.0593 a	0.570 ± 0.0442 a	0.525 ± 0.0400 a	
APPARENT SUCCESS				
% Nest starts hatched	72.5	77.8	69.8	100.0
% Hatched nests w/ 21d nestlings	89.5	80.4	86.1	55.6-66.7
% Nest starts w/ 21d nestlings	64.9	62.6	60.1	55.6-66.7
PRODUCTION STATISTICS				
Clutch size	3.0 ± 0.52 a[c]	3.1 ± 0.50 a	3.0 ± 0.56 a	3.3
Eggs hatched/nest start	2.1 ± 1.45 ab	2.2 ± 1.36 a	1.9 ± 1.43 (b)	2.7-3.1
Eggs hatched/hatched nest	2.7 ± 0.65 a	2.8 ± 0.65 a	2.5 ± 0.77 a	2.7-3.1
21d nestlings/hatched nest	1.6 ± 1.17 ab	1.7 ± 1.09 a	1.3 ± 1.12 (b)	0.9-1.6
21d nestlings/successful nest	2.1 ± 0.70 a	2.2 ± 0.64 a	1.9 ± 0.79 a	1.6-2.3

[a] Combined-species calculations except in 1992: Snowy Egret, Tricolored Herons, and Little Blue Herons in 1989; Snowy Egrets and Tricolored Herons in 1990 and 1991.

[b] Annual survival probabilities with the same letter cannot be separated using Bonferroni normal *z*-tests with $\alpha = 0.05$. Letters in parentheses indicate marginally significant differences separable at $\alpha = 0.10$. Hensler (1985) provides the formula for calculating *z* values. No tests for 1992.

[c] Production estimates with the same letter cannot be separated using Bonferroni *t*-tests with $\alpha = 0.05$. Letters in parentheses indicate marginally significant differences separable at $\alpha = 0.10$. No tests for 1992.

Snowy Egret and Tricolored Heron nest success and productivity remained more consistent through the study than was true for Great Blue Herons and Great Egrets. The maximum difference in overall Mayfield success through 21 days from 1989-1991 was only 10% for Snowy Egrets (53% in 1989, 60% in 1990, 51% in 1991, with no significant differences; Table 4-7) and only 4% for Tricolored Herons (54% in 1989, 57% in 1990, 53% in 1991, with no significant differences; Table 4-8). Estimates of hatching success were based on combinations of data for the two species (possibly including some Little Blue Heron failures in 1989), but were not identical because some segregation occurred within colonies. The hatching success estimates derived for Snowy Egrets ranged from 64-68%, and for Tricolored Herons from 60-66%, but there were no significant differences. The 1989 estimate for Tricolored Heron hatching success (60%) might have underestimated true success, because the unidentified nests from EBI were probably mostly Little Blue Herons. The latter achieved only 53% hatching success in 1989. Estimates of nestling-period success were species-specific, and among Snowy Egrets varied more than the estimates of hatching success. The 1989 and 1991 Mayfield probabilities of survival through 21 days for hatched Snowy Egret nests (78 and 80%, respectively) were not significantly different, but the probability was higher in 1990 (91%; significantly higher than in 1989, marginally higher than in 1991). In contrast, the estimates for Tricolored Herons did not vary significantly (89% in 1989, 86% in 1990 and 1991). Comparison of Apparent estimates of success revealed some variation in trends, but the only noteworthy difference was a relative decline in the estimate of nestling-period success for Snowy Egrets in 1989 (Table 4-7). The difference, however, did not significantly alter the conclusions about overall success.

All 1992 data were species specific, but the nest sample sizes were low in comparison to other years. The Apparent estimate of hatching success for Snowy Egrets in 1992 (90%) was precise, and ranked 11-17% higher than the combined-

species Apparent estimates for other years (Table 4-7). However, the possibilities for estimates of nestling-period success (38-73%) ranged from well below the estimates for other years to only slightly higher than the otherwise lowest estimate of 67% for 1989. Accordingly, the possibilities for Apparent estimates of overall success in 1992 (34-66%) ranged from very low to moderate in comparison to other years. The conclusions about Tricolored Heron success in 1992 were similar, but the very small sample size limited the reliability of the data (Table 4-8). All nine nests hatched eggs, so hatching success was 100% and ranked very high; however, only five or at most six of the nests survived to the 21-day nestling stage, so overall success ranged from 56-67% and ranked average compared to 1989-1991.

Each year 1989-1991, I confirmed that between 2.1-3.4% (2.9% overall) of the hatched Snowy Egret nests and between 0-1.4% (0.8% overall) of the hatched Tricolored Heron nests failed at >21 days posthatching (Table 4-6). However, between 40.7-66.0% (64.2% overall) of the hatched Snowy Egret nests and between 15.8-33.3% (32.4% overall) of the hatched Tricolored Heron nests produced one or more nestlings aged >21 days, but I was unable to verify whether any of the associated nestlings fledged (reached >35 days of age) or all perished. Thus, the estimates of 21-day nestling-period success overestimated the proportions of Snowy Egret (Table 4-7) and Tricolored Heron (Table 4-8) nests that fledged young by at least 1-4%, but the value may have been much higher. However, as I mentioned above for Great Egrets, a general lack of carcasses and the prevalence of fledglings in the colonies suggested that whole-nest failures were uncommon late in the nesting cycle.

Snowy Egrets averaged significantly larger clutches in hatched nests in 1989 (3.5) than in 1990 or 1991 (3.3 in both cases), and the mean clutch size in 1992 was intermediate (3.4)(Table 4-7). In contrast, there was no significant variation in clutch size among identified Tricolored Heron nests from 1989-1991 (range 3.0-3.1, with 1990 highest), but the mean clutch size of the 9 nests followed in 1992 was higher

(3.3)(Table 4-8). The higher 1989 mean clutch size among hatched Snowy Egret nests translated to a higher number of eggs hatched per nest start (2.4) and per hatched nest (3.2) compared to 1990 and 1991. However, the 1991 values (2.0 and 2.9) were statistically only marginally lower, and the only 1990 estimate that was significantly lower was the value for eggs hatched per hatched nest (2.8). Furthermore, despite higher egg production in 1989, the mean numbers of 21-day nestlings produced per hatched nest and per successful nest in 1990 (1.7 and 2.1, respectively) were higher--although not significantly so--than in 1989 (1.3 and 2.0)(Table 4-7). All Tricolored Heron production parameters were highest in 1990, but again no differences were significant at the $P \leq 0.05$ level (Table 4-8). Only the differences between combined-species estimates of eggs hatched per nest start (2.2 versus 1.9) and between estimates of 21-day nestlings produced per hatched nest (1.7 versus 1.3) approached significance.

The range of possible values for 1992 eggs hatched per nest start among Snowy Egrets (2.5-2.9) ranked high in comparison to the combined-species estimates for other years (in part a reflection of the moderately high mean clutch size; Table 4-7). The maximum possible estimate of eggs hatched per hatched nest also exceeded the values for other years, but the range of possibilities extended below all other estimates. The possible values for other production parameters ranged from low to only moderate in comparison to estimates for other years. Thus, hatching success and egg production among Snowy Egrets were probably moderately high in 1992, but nestling production was at best moderate and probably lower than in other years. The few Tricolored Herons studied in 1992 also averaged a higher number of eggs hatched per nest start (2.7-3.1) than in other years, and the range of values for eggs hatched per hatched nest extended from moderate to high in comparison to other years (Table 4-8). However, the range of possibilities for estimates of nestling production extended from

very low to moderately high in comparison to other years, so no definitive conclusions could be drawn.

The possible estimates of 35-day nestlings produced per hatched nest for Snowy Egrets ranged from 0.7-1.3 ± 0.9-1.0 in 1989, 0.9-1.7 ± 0.9-1.1 in 1990, and 0.6-1.5 ± 0.9-1.1 in 1991. Thus, the 21-day production statistics (Table 4-7) overestimated fledgling production per hatched nest for 1989 by 0.8-48.0%, for 1990 by 0-47.1%, and for 1991 by 0-60.9%. These wide margins certainly leave room for a change in conclusions relative to interannual comparisons, but the only way this would have occurred is if the post-21-day nestling mortality level in 1991 was conspicuously high. There was no reason to believe this occurred.

All 21-day old Tricolored Heron nestlings survived beyond 35 days in 1989; otherwise, the possible estimates of 35-day nestlings produced per hatched nest ranged from 1.5-1.7 ± 1.0-1.1 in 1990, and 0.9-1.3 ± 1.0-1.1 in 1991. Thus, the 21-day production statistics (Table 4-8) were an accurate reflection of fledgling production in 1989, but overestimated fledgling production per hatched nest for 1990 by 0-11.8%, and for 1991 by 0-30.5%. Thus, again the only possible change in the conclusions is that 1991 might have been a poorer year in terms of fledgling production than the 21-day statistics indicated.

Little Blue Herons. In 1989, I monitored the fate of 24 identified Little Blue Heron nests at the EBI colony, plus 23 unidentified nests that probably included a few Tricolored Herons. I also followed 10 identified nests at the MH colony, plus 24 unidentified nests that included a mixture belonging to all three species of small ardeids. This collection represented at best 12% (probably 7-8%) of the estimated peak number of nests built on the lake (Table 4-9). In 1990, I followed 21 nests at the EBI colony, and 27 nests at the CS colony, with no nests of uncertain identity (24% of the peak total). In 1991, the nesting population declined even more (Fig. 4-2), and in both 1991 and 1992 more of the nesting population occupied small isolated colonies

Table 4-9. Peak-total and marked nest counts, and nest success and productivity statistics by year for Little Blue Herons.

NEST COUNTS	1989	1990	1991	1992
Peak number of nests on-lake	685	202	62	124
Peak number of nests off-lake	80	110	35	15
Number of colonies monitored	2	2	1	0
Total Nests Monitored	81	48	6	0
Nests monitored - laying/incubation[a]	57	46	5	
Nests monitored - nestling period	37	42	5	
Nests w/ 21d nestlings	17	34	4	
MAYFIELD SUCCESS				
Laying/incubation[a]	0.467 ± 0.0741 b[b]	0.766 ± 0.0834 a	0.581 ± 0.3156 ab	
Nestling	0.411 ± 0.0817 b	0.809 ± 0.0607 a	0.789 ± 0.1872 ab	
Combined	0.192 ± 0.0492 b	0.619 ± 0.0821 a	0.458 ± 0.2780 ab	
APPARENT SUCCESS				
% Nest starts hatched	61.7	87.5	83.3	
% Hatched nests w/ 21d nestlings	46.0	81.0	80.0	
% Nest starts w/ 21d nestlings	28.3	70.8	66.7	
PRODUCTION STATISTICS				
Clutch size	3.2 ± 0.57 a[c]	3.4 ± 0.57 a	3.2 ± 0.75 a	
Eggs hatched/nest start	1.7 ± 1.46 b	2.7 ± 1.25 a	2.3 ± 1.21 ab	
Eggs hatched/hatched nest	2.7 ± 0.82 (b)	3.1 ± 0.76 a	2.8 ± 0.45 ab	
21d nestlings/nest start	0.7 ± 1.17 b	1.6 ± 1.11 a	1.2 ± 1.17 ab	
21d nestlings/successful nest	2.5 ± 0.62 a	2.1 ± 0.65 a	1.8 ± 0.96 a	

[a] Combined-species calculation in 1989 included Snowy Egrets, Tricolored Herons, and Little Blue Herons.

[b] Annual survival probabilities with the same letter cannot be separated using Bonferroni normal *z*-tests with $\alpha = 0.05$. Letters in parentheses indicate marginally significant differences separable at $\alpha = 0.10$. Hensler (1985) provides formula for calculating *z* values.

[c] Production estimates with the same letter cannot be separated using Bonferroni *t*-tests with $\alpha = 0.05$.

that I did not attempt to access. Consequently, I was able to follow only six nests at the EBI colony in 1991 (but 8% of the estimated on-lake total), and none in 1992.

Little Blue Herons initiated far more nests in 1989 than in other years (Fig. 4-2), but all estimates of nest success--both Mayfield and Apparent--and most estimates of production were lower in 1989 than in 1990 and 1991 (Table 4-9). However, these results were readily attributed to high, localized predation rates that happened to affect Little Blue Herons more than other species (see below for details). That this was true and conversely that production potential was not low, was confirmed by the fact that, although all 1989 estimates of nest success and production per nest start were significantly lower than in 1990, there were no significant differences in mean clutch size or in estimates of production per successful nest. Moreover, although the differences were not statistically significant, the 1989 estimate of 21-day nestlings produced per successful nest--the parameter that most reflects the quality of foraging conditions--was higher than for 1990 and 1991 (2.5, 2.1, 1.8, respectively).

I confirmed only one post-threshold, whole-nest failure from 1989-1991 (1.3% of the hatched nests; Table 4-6). Each year, between 13.3-47.6% (37.1% overall) of the hatched nests produced one or more nestlings aged >21 days, but I was unable to determine whether any nestlings fledged (reached >35 days of age) or all perished. Thus, there was very little evidence of late-stage failures, but again the estimates of 21-day nestling-period success (Table 4-9) could have overestimated fledging success by a substantial margin. The only possible change in conclusions is that the proportions of 1989 and 1990 nests for which fledging was verified were equivalent, whereas pre-threshold failures were 2.5 times more common in 1989 (Table 4-6).

The possible estimates of 35-day nestlings produced per nest start ranged from 0.5-0.7 ± 1.0-1.1 in 1989, 1.0-1.7 ± 1.1 in 1990, and 0.8-1.2 ± 1.2-1.3 in 1991. Thus, once again the 21-day production statistics (Table 4-9) might overestimate fledgling production by a considerable margin, but all ranges for the 42-day statistics include

values equal to the 21-day statistics (Table 4-9), so no definitive conclusions can be drawn.

White Ibises. I monitored 15 nests at EBI and 34 nests at MH in 1989 (9% of the estimated on-lake total; see Table 4-10), 85 nests at EBI in 1990 (9% of peak total), 96 nests at EBI in 1991 (23%), and 35 nests at EBI and 81 nests at MH in 1992 (13%; see Table 4-10). There were no statistically significant interannual differences in Mayfield hatching-period success from 1989-1991, but the estimate for 1989 of 47% was 13% lower than in 1990 and 9% lower than in 1991 (Table 4-10). In contrast, the Mayfield probability that a hatched nest produced at least one 14-day nestling was significantly higher in 1989 (87%) than in 1991 (64%), with the estimate for 1990 intermediate (80%) and not significantly different from the others (Table 4-10). Overall success was therefore lower in 1991 (36%) than in 1989 (41%), and highest in 1990 (48%), but no differences were significant. Apparent estimates of success revealed similar trends, but the hatching success estimate for 1989 was comparatively higher, which rendered an estimate of overall success equal to that for 1990 (Table 4-10). The 1992 Apparent estimate of hatching success was low in comparison to other years (50-51% versus 59-66% for 1989-1991), but nestling-period success was moderate to high (71-95% versus 66-86%). The resulting estimate of overall success (35-48%) nearly matched the range of values for other years (40-53%).

There were no significant differences between production estimates for 1989 versus 1990, and no consistent trends; however, all production estimates for 1991 were lower than in 1989 and 1990 (Table 4-10). The number of eggs hatched per successful nest was significantly lower in 1991 than in 1990 (2.3 versus 2.0, 1989 intermediate at 2.2), and the number of 14-day young produced per nest start was marginally lower in 1991 (0.9--same in 1989--versus 0.6). The number of young produced per successful nest was marginally lower in 1991 than in 1989 (1.8 versus 1.6, 1990 intermediate at 1.7). No other differences were statistically significant. The mean clutch size in 1992

Table 4-10. Peak-total and marked nest counts, and nest success and productivity statistics by year for White Ibises.

NEST COUNTS	1989	1990	1991	1992
Peak number of nests on-lake	565	1000	425	925
Peak number of nests off-lake	35	320	0	0
Number of colonies monitored	2	1	1	2
Total nests monitored	49	85	96	116
Nests monitored - laying/incubation	46	85	96	116
Nests monitored - nestling period	29	56	58	58-59
Nests w/ 14d nestlings	25	45	38	41-56
MAYFIELD SUCCESS				
Laying/incubation	0.468 ± 0.0795 a[a]	0.595 ± 0.0574 a	0.559 ± 0.0528 a	
Nestling	0.866 ± 0.0625 a	0.803 ± 0.0532 ab	0.644 ± 0.0633 b	
Combined	0.405 ± 0.0749 a	0.478 ± 0.0560 a	0.340 ± 0.0492 a	
APPARENT SUCCESS				
% Nest starts hatched	59.2	65.9	60.4	50.0-50.9
% Hatched nests w/ 14d nestlings	86.2	80.4	65.5	70.7-94.9
% Nest starts w/ 14d nestlings	51.0	52.9	39.6	35.3-48.3
PRODUCTION STATISTICS				
Clutch size	2.7 ± 0.48 a[b]	2.6 ± 0.62 a	2.5 ± 0.57 a	2.60
Eggs hatched/nest start	1.3 ± 1.23 a	1.5 ± 1.26 a	1.2 ± 1.12 a	0.9-1.2
Eggs hatched/hatched nest	2.2 ± 0.69 ab	2.3 ± 0.74 a	2.0 ± 0.76 b	1.8-2.3
14d nestlings/nest start	0.9 ± 0.99 ab	0.9 ± 0.95 a	0.6 ± 0.83 (b)	0.4-0.8
14d nestlings/successful nest	1.8 ± 0.47 a	1.7 ± 0.54 ab	1.6 ± 0.50 (b)	1.2-1.8

[a] Annual survival probabilities with the same letter cannot be separated using Bonferroni normal *z*-tests with $\alpha = 0.05$. Hensler (1985) provides the formula for calculating *z* values. No tests for 1992.

[b] Production estimates with the same letter cannot be separated using Bonferroni *t*-tests with $\alpha = 0.05$. Letters in parentheses indicate marginally significant differences separable at $\alpha = 0.10$. No tests for 1992.

equaled the moderate estimate for 1990 (2.6). Otherwise, all estimates for 1992 spanned ranges extending from considerably lower to moderate in comparison to other years, except that the maximum estimate for eggs hatched per nest start only equaled the lowest estimate for other years (i.e., 1.2 in 1991).

Each year from 1989-1991, between 0-6.9% of the hatched nests failed at >14 days posthatching (Table 4-6). However, between 31.0-67.7% (60.7% overall) of the hatched nests produced one or more nestlings aged >14 days, but I was unable to verify whether any of the associated nestlings fledged (reached >35 days of age) or all perished. Similarly, the ranges of possible estimates for fledglings (>35 days old) produced per nest start spanned from equivalent to generally well below the estimates of 14-day nestling production (0.7-0.9 ± 0.9-1.0 in 1989, 0.3-0.9 ± 0.6-1.0 in 1990, and 0.2-0.6 ± 0.6-0.8 for 21-day nestlings per nest start in 1991--lack of color-banding in 1991 meant too few confirmations to 35 days to warrant estimates). Thus, once again the threshold-based estimates of nestling-period success and production (Table 4-10) may have overestimated fledging success and fledgling production by considerable margins. Older White Ibis nestlings, especially those in low nests, were more prone than other species to jump and run when disturbed (pers. observ., discussed further below). I suspect that this increased the chance of drowning accidents (carcass lost from view) and cases of lost nestlings. Furthermore, the dark carcasses of the ibis nestlings were difficult to detect. Thus, there was reason to suspect a higher mortality rate and the chances of finding dead nestlings was low. In this case, therefore, I believe the threshold-based estimates probably did significantly overestimate true fledging success and fledgling production, perhaps by as much as 15-20%.

The proportion of nests confirmed to independence (>45 days) was much higher in 1989 (37.9%) than in 1990 (8.9%), suggesting that the pre-threshold failure levels underemphasized the fact that 1989 was a more successful year (Table 4-6). The same could be said about the 35-day nestling production statistics; the most likely

estimates were 0.78 per nest start for 1989 and 0.67 for 1990, whereas the 14-day statistics were more equal--0.94 in 1989 and 0.92 in 1990. Drawing the 1991 statistics into the comparisons is less justifiable, because I did not color band ibises in 1991, and so the chance of advanced-age confirmations was reduced.

Comparisons with other regional data. Frederick and Collopy (1988) estimated Mayfield success for 59 Great Blue Heron nests in one Everglades colony in 1987; all measures were lower than observed in any season during this study, with the exception that incubation-period success in 1990 was low at Lake Okeechobee. No other recent statistics from southern Florida were available for comparison. Compared to birds studied in several colonies in the Everglades from 1986-1989 (Bancroft et al. 1990; Frederick and Collopy 1988, 1989a), Great Egrets also generally did well for southern Florida during this study. In contrast, Snowy Egret success and productivity ranked only moderate compared to similar statistics for several southern Florida colonies studied from 1986-1989 (same authors) and in 1992 (Frederick 1993). Nesting success and productivity varied much more among Tricolored Herons studied in the same 1986-1989 and 1992 Everglades colonies than at the lake. The Everglades cases included several whole-colony failures, but otherwise successful colonies generally averaged higher nest success than those at the lake. Nest success also varied considerably among Little Blue Herons studied in the Everglades. In comparison, birds at the lake achieved average success and moderately high nestling productivity in 1989 and 1990, but did poorly in 1991. White Ibis nest success at Lake Okeechobee was more consistent and productivity was at least moderately high compared to the previous several years in the Everglades (same authors). Data gathered at Loxahatchee National Wildlife Refuge (H. Jelks pers. comm.) also indicated that White Ibis productivity at the lake in 1990 and 1991 was at least moderate in comparison.

Causes of Nest Failure

Identifying causes of failure. Table 4-11 lists the proportions of failed nests and the probable proximate causes of nest failure documented through observations at nest sites from 1989-1991. I did not include data for 1992 for two reasons: the frequency of visits was low and therefore it was more difficult to assign causes of nest failure, and excluding the 1992 data insured that the results represented the same set of data analyzed by logistic regression in Chapter 5. I often could not ascertain the proximate cause of nest failure at the nest; consequently, many failures were labeled as either scavenged after abandonment or taken by a predator. I identified a more specific cause of failure for 62% of the failed Great Blue Heron nests, for 29% of the failed Great Egret nests, for 45% of the Snowy Egret nests that failed with nestlings, and for 25% of the failed White Ibis nests. In addition, as alluded to above, several Little Blue Heron nests with young probably failed because of predators, but definitive proof was usually lacking (discussed further in next section).

Losses due to abandonment. Abandonment was the leading, identifiable proximate cause of failure for all species except perhaps Little Blue Herons (Table 4-11). This result was consistent with the findings of Frederick and Collopy (1989a, b). Abandonment was particularly common among the largest two species. A total of 46% of the whole-nest losses for Great Blue Herons were the result of abandonment, with 8% percent possibly involving disease. A total of 21% of all confirmed Great Egret failures were due to abandonment.

Losses due to Predation. There was no evidence that predation played a role in the losses of Great Blue Heron nestlings, but Fish Crows (Corvus ossifragus) and Boat-tailed Grackles (Quiscalus major) destroyed some eggs of all species. Crows are well-known predators of wading bird eggs and small nestlings (Shields and Parnell 1986; Bancroft and Jewell 1987; Frederick and Collopy 1989b; Bildstein et al. 1990).

Table 4-11. The fate of marked nests and causes of nest failure by species: 1989 - 1991.

	Great Blue Heron	Great Egret	Snowy Egret	Tricolored Heron	Little Blue Heron	Unidentified Small Ardeid	White Ibis	Totals
Nests Monitored	173	548	256	171	90	129	228	1595
Nests Fledged	97	259	192	123	56	0	110	837
Nests w/ Fate Uncertain	0	0	11	1	0	0	4	16
Incubation Failures								
scavenged/predated	19	164	12	22	9	107	66	399
abandoned	19	59	1	3	2	11	17	112
wind blown	10	13	0	0	0	0	0	23
poor nest structure	1	5	0	0	0	1	0	7
Totals	49	241	13	25	11	119	83	541
Nesting Period Failures								
scavenged/predated	12	43	22	16	20	10	19	142
abandoned	9	2	10	2	0	0	6	29
predated	0	2	8	1	2	0	5	18
disease/abandonment	6	0	0	1	1	0	0	8
disease	0	0	0	1	0	0	0	1
wind blown	0	1	0	1	0	0	1	3
Totals	27	48	40	22	23	10	31	201

Grackles have not been commonly implicated as wading bird egg predators, but there was no question that some individual egg losses were due to grackles that took advantage of adults moving off their nests when disturbed by a human presence. The larger wading bird species were probably capable of defending their nests against marauding crows and grackles, and observed egg depredations might have occurred only because attendant adults were disturbed from their nests during colony checks. Individual eggs definitely were destroyed by avian predators; however, I was never able to assign avian predation as the definitive cause of a whole-nest loss during incubation (Table 4-11), because I could never rule out post-abandonment scavenging as a possibility.

For Great Egrets, the only two cases of nestling-period failure labeled as predation in Table 4-11 probably involved raptors. One case probably involved a Red-tailed Hawk (Buteo jamaicensis) at EBI. On one occasion I saw the resident hawk carrying a fresh-killed, adult Snowy Egret. In the other case, I had seen a wintering Peregrine Falcon swooping over the colony on several occasions, and evidence such as plucked feathers and broken neck bones suggested the involvement of a falcon. A large Great Egret fledgling from a nearby unmarked nest was killed in the same fashion. There was also much evidence that Red-shouldered Hawks and crows were involved at least as scavengers if not predators at the HP colony, which Great Egrets gradually abandoned in 1989.

As mentioned previously, the low nestling period success of Little Blue Herons in 1989 (Table 4-9) was likely a result of predation. Although probably not regularly a significant cause of nest loss (Frederick and Collopy 1989b), predation did greatly affect the 1989 nest success estimates for Little Blue Herons because of the modest nest sample size. Avian predators were likely responsible for losses at EBI; 9 of 18 marked nests that hatched eggs lost all nestlings abruptly and without a trace within the first week of hatching. Both Red-tailed Hawks and Black-crowned Night Herons were

positively identified as wading bird predators at EBI during the study, and were likely involved in this instance. A pair of Red-tailed Hawks lived near the colony throughout the study period, and I was able to confirm that raptor predation was the cause of loss at one Little Blue Heron nest in 1990 (I recovered the USFWS bands from two siblings in a raptor regurgitant pellet very near the nests involved). Black-crowned Night Herons always nested in small numbers at EBI during the study, and are well known predators of small nestlings (Frederick and Collopy 1989b). In 1991, two night heron nestlings regurgitated several small Cattle Egret chicks at EBI; otherwise, I was unable to confirm specific night heron predation events. At the Moore Haven colony in 1989, an alligator(s) was positively responsible for the loss of one whole brood of Little Blue Herons, and probably was involved in the loss of at least three of the other four nests that failed with young nestlings. Thus, although I only listed two losses as definitely due to predation, I suspected that predation was responsible for most of the other 20 Little Blue Heron nest failures listed as scavenged or predated (Table 4-11).

The eight cases of predation involving Snowy Egret nestlings, the one for Tricolored Herons, and two of the five cases for White Ibis nestlings (Table 4-11) definitely involved the same alligator(s) implicated in the loss of Little Blue Heron nestlings at the MH colony in 1989. Two of the remaining White Ibis losses likely involved a raptor and a crow, but there were no clues to the identity of the third predator. I confirmed no other cases of predation among marked Snowy Egret or Tricolored Heron nests, but circumstantial evidence suggested that nesting Black-crowned Night Herons took several whole broods of young nestlings at EBI, particularly in 1991. This was probably the reason why a logistic regression analysis revealed a negative association between the probability of nest failure and overhead vegetative cover for Tricolored herons during the nestling phase (Chapter 5). The regression analyses also revealed a significant positive correlation between nest failure and nest height, and a negative correlation with nest cover among incubating Snowy Egrets and

Tricolored Herons (combined-species analysis). In the latter cases, the combination of greater nest height and exposure probably rendered the nests more susceptible to egg predation by crows and grackles. Again, however, no whole-nest losses during incubation could be unequivocally labeled as the result of predation.

I alluded to the possibility that drought-related invasions of terrestrial predators might have contributed to the mid-season abandonment of the IP colony in 1989. The Great Egret failures probably resulted in large part because cold temperatures and sudden increases in the lake stage reduced foraging efficiency (discussed further below). However, a visit to the colony shortly after the abandonment revealed almost no egg remains despite there having been many nests with eggs. This fact suggested that raccoons (Procyon lotor) or other mammalian predators/scavengers had invaded the colony and carried off the eggs, although snakes such as the Eastern Cottonmouth (Agkistrodon piscivorus) or Rat Snake (Elaphe obsoleta) could also have scavenged eggs without leaving remains. Water depths in the marshes around the colony had declined significantly by the time the Great Egrets abandoned, and this might have increased accessibility for mammalian predators or scavengers. The Little Blue Herons and other species initiated nesting a month after the Great Egrets and Great Blue Herons had departed, and by then the mean lake stage had dropped another 0.3 m and much more of the surrounding marsh had dried. The chance of invasion by mammalian predators was therefore higher, and the eventual abandonment by all the Cattle Egrets, as well as the other species, provided further evidence that predators were a problem. Cattle Egrets are more terrestrial in their feeding habits (Palmer 1962; Hancock and Kushlan 1984), and therefore would not have responded the same to changing hydrologic or climatic conditions that might have affected the foraging efficiency of other species.

Losses due to disease and parasites. Necropsy results implicated disease and parasitism in several cases of individual nestling mortality (Spalding et al. 1994; unpubl.

data), but whole-brood failures due to disease were not common, or at least not easily confirmed. I assigned disease as the cause of whole nest failure only if the last remaining nestlings perished because of disease. In the one case listed for Little Blue Herons (Table 4-11), a parasitic infection of Eustrongylides ignotus (Spalding and Forrester 1993; Spalding et al. 1993, 1994) resulted in the death of the last surviving nestling. Eustrongylidosis was also the cause of failure in one of the Tricolored Heron cases (Table 4-11). The other Tricolored Heron loss was probably due to combinations of liver, lung, and/or kidney disease in the two oldest nestlings. The six cases listed for Great Blue Herons involved a variety of conditions including a congenital heart defect, metabolic bone disease, intestinal disease, and eustrongylidosis.

Behavior-related losses among White Ibises. White Ibis nestlings were particularly prone to scatter erratically from their nests when approached (pers. observ.). This might have proved particularly lethal in 1991--when nestling-period success and nestling production were lowest (Table 4-10)--because the primary colony at EBI was underlain by a deep, soupy-muck substrate in which nestlings might have drowned. This tendency was probably the reason for nest height appearing as a significant determinant of nest failure in the logistic regression analysis discussed in Chapter 5. A negative association indicated low nests failed more often, probably because nestlings in higher nests usually just climbed higher in the willows as opposed to jumping and running off. I did not handle White Ibis nestlings in 1991 for banding and measuring, and so the level of stress I caused should have been lower than in previous seasons.

Losses related to climate and hydrology. The larger two species were the only ones for which wind damage--toppled nest trees and dislodged eggs--was a significant cause of nest failure (14% for Great Blue Herons, 5% for Great Egrets; Table 4-11). A logistic regression analysis revealed that nest height was a significant determinant of

nest failure among Great Blue Herons (positive correlation; Chapter 5), reflecting the fact that high nests were more likely to be negatively affected by high winds. Frederick and Loftus (1993) also found that high winds associated with late-winter storm fronts were a significant cause of nest failure among Great Egrets in the Everglades. In addition, it appeared that five pairs of Great Egrets (2% of failure), one pair of Great Blue Herons, and one pair of either Snowy Egrets or Tricolored Herons lost their eggs at the lake because their nests were poorly built (Table 4-11), but high winds could have exacerbated the problem.

Species-specific plots illustrating the timing of marked nest failures during the 1989-1991 seasons are shown in relation to plots of the mean daily lake stage, total daily rainfall, and the minimum daily air temperature in Figure 4-3. As noted above, the Mayfield probability of survival through incubation for Great Egrets in 1989 was very low. Six percent (6 of 99) of the marked nests failed during a 4-day, 11-15°C drop (compared to the mean for the previous 30 days) in minimum daily temperatures that occurred in late February (Fig. 4-3). Four days later, a 12-day, 0.10 m reversal in what had previously been a relatively steady and rapid surface-water recession began (0.82 m drop over the previous 30 days; Fig. 4-3). Late winter cold fronts dropped an average of 5.75 cm of rain on the lake over 10 days (Fig. 4-3), and contributed even more to increasing the lake stage because Lake Okeechobee drains a 12,000 km^2 upstream watershed (Aumen 1994). Moreover, the fronts produced two more 5-6°C drops in minimum temperatures over a three day period near the end of the reversal. Another 8% of the marked Great Egret nests failed during the reversal period, and an additional 35% of the Great Egret and 24% of the marked Great Blue Heron nests failed within two weeks of the events. The Great Egret failures included 62% of the marked nests with eggs at EBI (plus 4 nests with small nestlings), 50% of the incubated nests at MH (plus 2 nests with small nestlings), and all of 45 nests (21 marked, 13 with

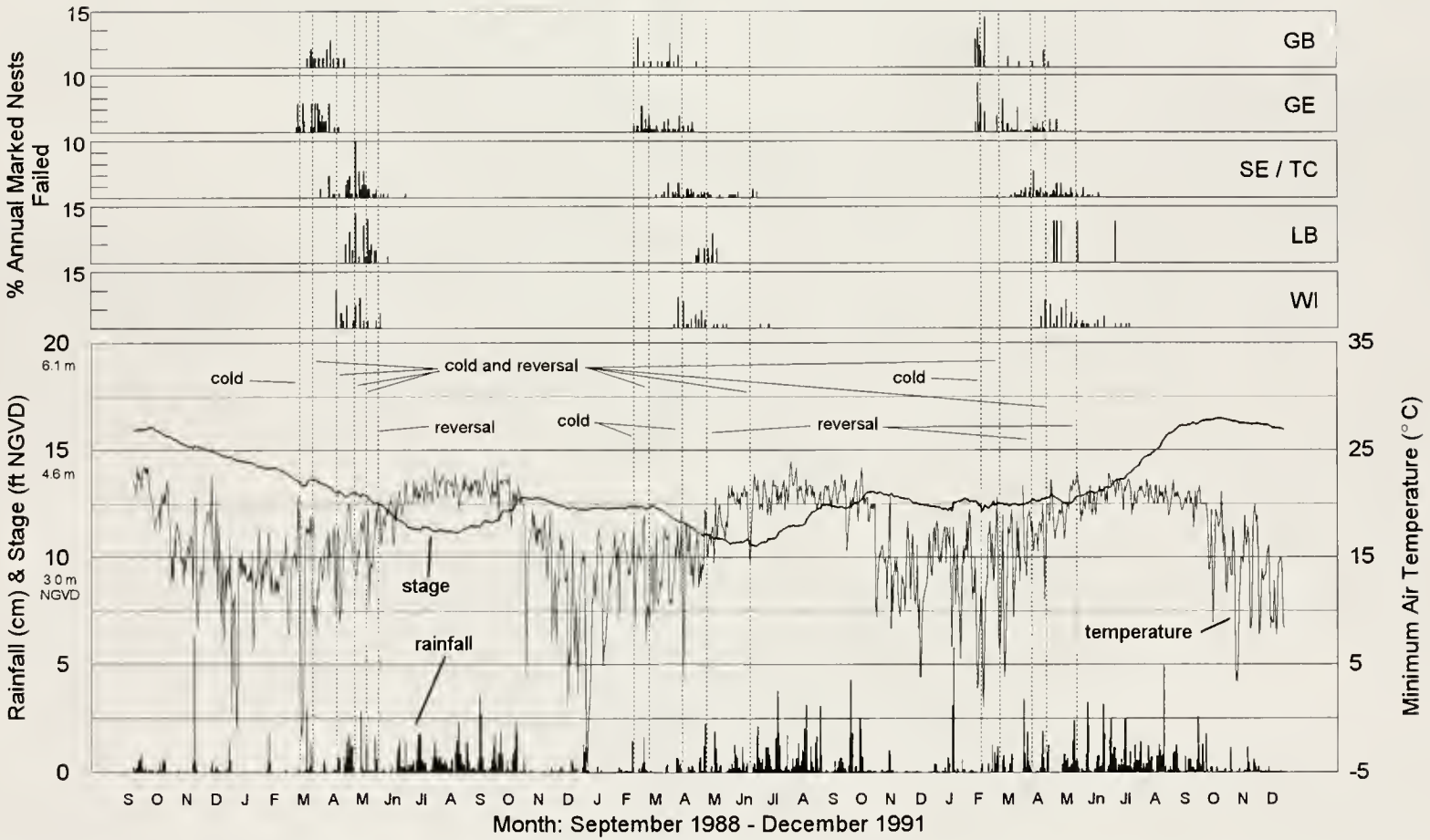

% Annual Marked Nests Failed
GB
GE
SE / TC
LB
WI
Rainfall (cm) & Stage (ft NGVD)
Minimum Air Temperature (° C)
cold
cold and reversal
cold
reversal
cold
reversal
stage
rainfall
temperature
6.1 m
4.6 m
3.0 m NGVD
S O N D J F M A M Jn Jl A S O N D J F M A M Jn Jl A S O N D J F M A M Jn Jl A S O N D
Month: September 1988 - December 1991

Figure 4-3. Timing of nest failures, 1989-1991, in relation to trends in daily lake stage, rainfall, and minimum air temperature. Dashed vertical lines mark occasions when cold temperatures and reversals in surface-water recessions led to higher nest failure rates. Upper plots indicate the percentages of marked nests--calculated over annual totals--that failed on a given date, and are labelled on the right with species codes: GB = Great Blue Heron; GE = Great Egret; SE / TC = Snowy Egret and Tricolored Heron combined; LB = Little Blue Heron; WI = White Ibis.

eggs) at the HP colony (Fig. 4-1). In addition, all the Great Egret nests at the IP site (80 incubated nests, 145 courting pairs) were abandoned during this time.

The 1991 season also featured two periods of cold weather that affected Great Blue Herons and Great Egrets. The first, in mid-February, involved a 7-day period of cold during which the minimum daily temperature twice dropped 12-13°C lower than the previous 30-day average (Fig. 4-3). The cold front also brought persistent high winds (no precise data) that, as mentioned above, snapped the tops of willow trees containing especially Great Blue Heron nests and dislodged eggs from others. The combination of cold and wind precipitated the abandonment of all the Great Egret and Great Blue Heron nests in the first wave of nesting at EBI (120 and 55 nests, respectively, all with eggs and including 57% and 44% of the total marked nests; Fig. 4-3). All but 15 of 75 Great Egrets that had just begun to nest at the MH colony also at least temporarily abandoned the effort; however, 37 pairs of Great Blue Herons nesting at the OTI site and 95 pairs of Great Egrets at the LH site did not abandon (Fig. 4-1). My presence in the EBI colony around the time of the events could have contributed to the full-scale abandonment there (English 1978; Gibbs et al. 1987; Kelly et al. 1993). I had not yet visited the OTI site and never visited the LH site, but I also had not visited the abandoned MH site. The second period of cold began on 5 March, involved two 9-10° C drops in minimum temperatures over 8 days, and followed an unsteady, 14 day, 0.16 m increase in the lake stage. Another 11% (34 of 279) of the total number of marked Great Egret nests failed coincident with these events (Fig. 4-3).

Nest failures among Great Blue Herons in 1990 were less easily ascribed to particular climatic or hydrologic events, but 20% of the marked Great Egret nests (34 of 169) failed during a 10-day period when two 5-6°C drops in minimum daily temperatures and a minor fluctuation in the mean lake stage occurred (0.03 m drop followed by a 0.05 m increase; Fig. 4-3).

Thus, there was strong correlative evidence that cold temperatures and increasing surface-water levels negatively affected both Great Egrets and Great Blue Herons in 1989 and 1991, and probably in 1990 as well. Great Egret hatching success was most affected in both years. Great Blue Heron hatching success was strongly reduced in 1991, but in 1989, 8 of the 10 Great Blue Heron nests that failed already had nestlings, and so the estimate of nestling-period success was most affected (Table 4-4). Frederick and Loftus (1993) demonstrated that during cold weather forage fishes are more likely to remain hidden and inactive, and to seek shelter sooner when disturbed. They speculated that protracted cold snaps might therefore sufficiently reduce wading foraging efficiency as to cause nest failures. It is less likely that cold temperatures affected the incubating birds directly (Simmons 1959). The sudden increase in lake levels probably allowed prey to disperse and thereby further reduced foraging efficiency (Kushlan et al. 1975). However, as noted above, predation pressure might have helped spur the abandonments that occurred at the IP and HP colonies.

During this study, the smaller ardied species generally did not abandon their nesting efforts en masse after having invested in the effort for an extended period (i.e., most nests with eggs or young). I already mentioned one exception involving the Little Blue Herons and Cattle Egrets at the IP colony in 1989. Another minor exception occurred in 1991 at the small satellite willow head considered part of the MH colony. This case involved 25 pairs of Snowy Egrets, some of which probably laid eggs (15 pairs of White Ibises and 5 pairs of Tricolored Herons were also observed at the site, but only on one survey). Otherwise, although mid-cycle abandonments were not common, several cases of pre-incubation abandonment did occur, particularly during the high-water season of 1992 (Table 4-3).

On one occasion in 1991, a large group of 300 Snowy Egrets began courting along with some relocated Great Egrets in the willows on the dike next to EBI, but all the Snowy Egrets aborted within a week without building nests. Most of these birds

probably joined a renewed effort within a month on the main island, and the event might simply have reflected the fact that Snowy Egrets never initiated a nesting attempt without there being other species such as Great Egrets already present. The original Great Egret efforts were interrupted by a cold front and some birds had attempted to renest at a non-standard location, ultimately unsuccessfully; the Snowy Egrets might simply have been temporarily lured to an unsuitable location. In 1992, however, an overall reduction in nesting attempts (Fig. 4-2), generally lower estimates of nest success and productivity (Tables 4-4 - 4-10), and the increase in aborted attempts (Table 4-3) all suggested that foraging conditions were poor due to the high water conditions. Otherwise, I highlighted some additional cold snaps and reversals in Figure 4-3 that coincided with periods of nest failure among the small ardeids from 1989-1991; however, compared to evidence presented for Great Blue Herons and Great Egrets, it was less possible to visually correlate specific bouts of failure with specific climatic or hydrologic events.

As I mentioned above, White Ibises initiated unsuccessful late waves of nesting in July 1991 and 1992. The initiation of the 1992 wave corresponded to an abrupt and rapid decline in surface-water levels (Fig. 4-2). However, the recession was brief, and in both 1991 and 1992 the proximate cause of failure for the late nests was the onset of heavy summer rains (see Fig. 4-3 for the timing of rainfall in 1991). The heavy rains may have reduced the adults' ability to maintain the quality of their nests, but it is more likely that rapidly increasing water levels reduced the quality of foraging conditions and forced abandonment (Kushlan et al. 1975; Frederick and Collopy 1989a).

The logistic regression analyses discussed in Chapter 5 confirmed the importance of cold temperatures as a cause of nest abandonment/failure, for all species but most notably for Great Egrets during incubation. The regression models also confirmed the universal importance of hydrologic trends in determining the availability and quality of foraging opportunities and therefore the probability of nest

failure. The relationships shown often were complex and varied by species, but the general conclusion was that the probability of nest failure among all species was lowest during periods of surface-water recession. Great Blue Herons and Little Blue Herons appeared to prefer slower rates of recession, but Great and Snowy Egrets preferred faster rates, and all species were negatively affected by abrupt reversals in established drying trends. High-volume, short-duration rainfall events usually increased the probability of nest failure, but consistent, lower-volume rainfall events probably insured the persistence of ephemeral wetlands and isolated prey populations, especially during the drought.

Conclusions and Management Implications

Higher numbers of nest initiations in both 1989 and 1992 suggested that Great Egrets and Great Blue Herons were attracted by the combination of high winter surface-water levels and an early spring recession. A preference for higher surface-water levels among Great Blue Herons is consistent with long-term data indicating that the species' nesting effort has at least remained stable if not increased since a higher lake-stage regulation schedule was adopted in 1978 (David 1994a). However, the per nest productivity of both species was highest in 1990 when the number of nest initiations was lowest. Perhaps the early season environmental cues were sufficiently misleading in 1990 and 1991 to have deterred potential nesters. Before both species initiated nesting in 1990, the lake stage had remained fairly stable and at a low level for much of the winter (Fig. 4-2). There was more of a drying trend through the winter of 1990/91, but the lake stage still had remained much lower than at the beginning of both the 1989 and 1992 seasons. Severe droughts do not occur regularly. If these species rely on deeper water to support larger prey (Meyerricks 1962; Willard 1977), but also profit from the prey-concentrating effects of receding water (Kushlan 1976b), instinct

might dictate that low, stable surface-water levels in late winter will mean poor foraging conditions in the spring. The smaller species, on the other hand, did not initiate nesting in 1990 until after the recession had begun (Fig. 4-2), and so might have been able to better anticipate the potential, unexpected benefits and accordingly initiate more nests than in 1989.

The reproductive effort of Little Blue Herons was high in 1989, but declined thereafter. Little Blue Herons also differed from Great Egrets and Great Blue Herons in that, the productivity of Little Blue Heron nests that succeeded in 1989 was highest for the study. A regression analysis of the probability of nest failure during the nestling phase (Chapter 5) indicated a positive correlation between nest failure and lake stage. Therefore, high water per se was not an advantage for nesting Little Blue Herons feeding young. However, the 1989 season was preceded by several years of high water, whereas the 1992 season was preceded by a two-year drought and one year of only moderate lake levels (see Richardson and Hamouda 1994 for a long-term hydrograph). Loftus et al. (1990) and Loftus and Eklund (1994) provided evidence that long hydroperiod marshes in the Everglades support higher densities of small fishes and some macroinvertebrates than similar short hydroperiod marshes. One of the most dramatic effects was shown for grass shrimp (or prawns, in their terminology), which constituted nearly 50% of the aggregate mass of prey fed to Little Blue Heron nestlings at Lake Okeechobee in 1989 (McIvor and Smith 1992). Other species also fed on grass shrimp, but not to such a great degree. Thus, several years of high water probably allowed the Little Blue Herons' primary prey to proliferate throughout the littoral zone. The drought then produced a rapid and large-scale surface-water recession during the 1989 nesting season that both brought water depths down to acceptable levels and served to greatly concentrate the abundant grass shrimp. The nesting birds would thereby have had access to a rich and preferred food supply.

The 1990 season also featured a rapid surface-water recession that concentrated prey. Quantitative sampling (not done in 1989) revealed high densities of grass shrimp--as well as small fishes--in deeper habitats, primarily beds of submerged vegetation (McIvor and Smith 1992; Chick and McIvor 1994). Foraging-dispersion surveys revealed that all species were strongly attracted to such habitats during peak drought periods (Chapter 2, 3), and even deep water areas were accessible because the proliferation of thick, surface mats of Hydrilla (Zimba et al. 1994) and clumps of water hyacinth provided extra support (Chapter 2). Little Blue Heron nest numbers declined in 1990, perhaps because the variety of acceptable colony sites and foraging grounds was reduced by the drying of the interior marshes, but the productivity of those pairs that chose to nest remained high. Conversely, surface-water levels increased some prior to the 1991 season and no protracted recession occurred. This allowed prey organisms to disperse and, in response, Little Blue Heron nest numbers declined even further and productivity dropped.

The reproductive effort of Snowy Egrets and especially Tricolored Herons was highest for the study in 1990, but was also higher in 1991 than in 1989 or 1992 (Fig. 4-2). The lake stage was approximately equal each year from 1989-1991 at the time these two species began to nest, suggesting that the early-season high water might have been the cue to discourage some potential breeders from remaining on the lake in 1989. The higher effort in 1990 was undoubtedly a response to the low and declining lake levels that enhanced foraging conditions (Chapters 2, 5), but the higher effort in 1991 may have been a result of habitat selection independent of direct hydrologic influences. A variety of new vegetation complexes emerged in the wake of the 1989/90 drought (Richardson and Harris 1994). Most importantly, the aforementioned proliferation of highly productive (McIvor and Smith 1992; Chick and McIvor 1994) mats of Hydrilla, and the expansion of beds of lotus underlain by Hydrilla, attracted many foraging birds (Chapter 2). Shallow Hydrilla flats in Fisheating Bay and around Eagle

Bay Island and King's Bar (the island just south of EBI; see Fig. 4-1) attracted all species and record numbers of non-nesting birds (Chapter 2) in 1990 when the drought had concentrated prey in these areas. However, in 1991 after the lake stage had risen again to moderate levels, Snowy Egrets and Tricolored Herons--and a few aerial foraging Great Egrets--were generally the only species that still fed in the lotus and Hydrilla habitats. My observations suggested that Tricolored Herons were particularly attracted to the mixed lotus and Hydrilla habitats, where they used the large surface leaves of the lotus plants for support while fishing in the underlying Hydrilla. Snowy Egrets used both habitats, but were most attracted to the thick Hydrilla mats and areas where clumps of water hyacinth served as platforms from which the birds launched aerial dipping runs (sensu Hancock and Kushlan 1984). In 1992, the lake stage returned to high levels, and most of the thick surface mats and patches of lotus and hyacinth disappeared. Then even the Snowy Egrets and Tricolored Herons were forced to search elsewhere for productive foraging opportunities.

High reproductive effort and nest productivity suggested that White Ibises were also attracted by the low and declining lake levels of 1990. Moreover, although reproductive effort was lower in 1989, there were no significant differences between 1989 and 1990 estimates of nest success and productivity. In contrast, both reproductive effort and nest productivity were low in 1991 in the absence of a protracted surface-water recession. Moreover, at least the first peak in ibis nesting during 1991 appeared to correspond to a brief dip in surface-water levels (Fig. 4-2). White Ibis reproductive effort was higher in 1992 than in 1991, and 1992 productivity was at least nearly equal if not higher than in 1991. The 1992 season featured periods of pronounced surface-water recession, and both peaks in nest numbers coincided with rapid declines in the lake stage (Fig. 4-2). Thus, there was strong correlative evidence that low stages and particularly receding surface-water levels enhanced ibis foraging efficiency, either by providing concentrated food sources or by increasing access to a

wider variety of foraging habitats. The logistic regression analyses conducted by both myself (Chapter 5) and Frederick and Collopy (1989a) also confirmed that the success of White Ibis nesting often depends on rapid surface-water recessions, but in neither case was absolute water depth as important a predictor.

In summary, steadily declining and lower lake stages associated with a two-year drought cycle generally enhanced all species nest productivity. The timing and magnitude of Great Egret and White Ibis nesting efforts appeared particularly sensitive to the occurrence of surface-water recessions. However, the interannual pattern of variation in the reproductive effort of Great Blue Herons and Great Egrets matched neither the patterns of variation in nest productivity nor the patterns of variation in the abundance of the larger foraging population (Chapter 2). This fact suggested that these species ability to forecast future foraging conditions was compromised by the unusually severe drought. Little Blue Herons were unique in that it appeared long-term antecedent hydrologic conditions played a dominant role in determining the species' nesting population responses. Snowy Egrets and Tricolored Herons were unique in that they appeared to achieve a level of independence from on-lake hydrologic conditions in 1991 by using floating vegetation for support while foraging in prey-rich habitats too deep for wading. In general, however, although unpredictable predation, disease, accidents, wind events, and particularly cold-temperature events all influenced the success of some species nesting efforts, potentially manageable surface-water trends were of primary importance with regards to the nesting and foraging dynamics of all species. All species achieved at least moderately high levels of nest success and productivity, and reproductive effort of several species was highest in 1990 when the lake stage was low and declining steadily. However, the widest variety of suitable nesting colony sites was available in 1992 with high water levels. In contrast, the intermediate lake levels of early 1989 and in 1991 provided both a moderately wide variety of suitable nesting sites and a wide array of accessible foraging habitats.

This and other evidence (Chapter 2; Chapter 5) suggests that the best management strategy would be to encourage moderately high winter stages followed by a moderate-paced, steady, and protracted (5-6 month) surface-water recession beginning in December or January. However, periodically allowing surface-water levels to remain high for 2-3 years may enhance the growth of certain prey populations and thereby yield maximum benefits to foraging wading birds when followed by a large-scale recession. Conversely, periodically allowing the lake stage to reach low levels will expose and encourage the expansion of highly productive beds of submerged vegetation (Zimba et al. 1994), will insure the persistence of healthy willow stands that serve as nesting substrate (David 1994a; Richardson and Harris 1994), will encourage the development of successional complexes of vegetation that attracted several species for foraging (Chapter 2), and will allow fires to clear thick and unproductive cattail and Panicum wrack (Chapter 2; Richardson and Harris 1994). In general, pronounced intra- and interannual hydrologic fluctuations and periodic disturbances such as freezes and fires may be the key to insuring the persistence of diverse and productive vegetation assemblages (Gunderson 1994), and therefore diverse and healthy prey and wading bird populations. Finally, data presented in Chapter 3 indicated that some nesting wading birds at the lake consistently rely on off-lake foraging habitats regardless of hydrologic conditions on the lake. Thus, managers should realize that regulation of lake water levels may ultimately affect the abundance of foraging birds on the lake more than nesting populations, and management plans should recognize that adjacent wetland habitats are an important resource for birds that nest on the lake.

CHAPTER 5
ENVIRONMENTAL DETERMINANTS OF NEST FAILURE: LOGISTIC REGRESSION ANALYSES

Introduction

The history of hydrologic manipulation in Florida is extensive (Light and Dineen 1994), and evidence suggests that hydrodynamic changes and wetland habitat alterations have led to substantial declines in the nesting populations of most wading bird species (Kushlan and White 1977; Ogden 1978a, 1994; Kushlan et al. 1984; Kushlan 1986a, 1987; Kushlan and Frohring 1986; Walters et al. 1992; Bancroft et al. 1994; Frederick and Spalding 1994). For instance, Wood Storks often appear to rely on the maintenance of specific surface-water levels and on prolonged and rapid spring surface-water recessions to produce and concentrate enough prey to sustain successful nesting (Kahl 1964; Kushlan et al. 1975; Browder 1976; Clark 1978; Ogden et al. 1978; Bancroft and Jewell 1987; Frederick and Collopy 1988). Changes in the timing and annual pattern of surface-water fluctuations has led to a significant shift toward later nesting among Wood Storks, which means that heavy summer rains that disperse prey often begin before nestlings attain independence (Kushlan et al. 1975; Ogden 1994). However, Ogden (1994) presented evidence that Wood Storks may have only recently become dependent on rapid recession rates. He suggests that the storks have been forced to rely more heavily on the prey-concentrating effects of rapid recessions, because human alteration of flow patterns has degraded the quality of the Everglades prey base (Loftus and Eklund 1994).

There is also compelling evidence that reversals in established surface-water recession trends negatively affect the reproductive effort, timing, and success of White Ibises, because the reversals disperse prey and/or reduce the accessibility of primary prey species (e.g., crayfish in the Everglades; Kushlan 1976c, 1979; Frederick and Spalding 1994). Frederick and Collopy (1989a) concluded that "drying rate is important both as a short-term prerequisite for White Ibis nest initiation ... and as a determinant of nesting success." However, in South Carolina, high spring rainfall led to high reproductive effort among White Ibises, because high rainfall maintained ephemeral, freshwater wetlands that supported dense crayfish populations (Bildstein et al. 1990). In addition, Kushlan (1979) noted that when water levels were rising White Ibis in the Everglades tended to move to newly flooded areas, and he suggested that water depth rather than the direction of water level change may be the most important habitat selection factor for the species.

Unlike for storks and ibises, few studies have documented the unequivocal dependence of ardeid nest success on freshwater hydrologic trends. In the Everglades, the passing of cold weather--often but not always including high rainfall--and the onset of heavy summer rains has resulted in synchronous colony abandonments by Great Egrets, Snowy Egrets, and Tricolored Herons (Bancroft and Jewell 1987; Frederick and Collopy 1989a; Frederick et al. 1992; Bancroft et al. 1994; Frederick and Spalding 1994). The logistic regression analysis conducted by Frederick and Loftus (1993) indicated that high rainfall, cold temperatures, and high winds--all associated with late-winter cold fronts--were significant positive determinants of nest failure for Great Egrets in the Everglades. The same regression analysis failed to implicate water depth and surface-water drying rate as significant influences. Maddock and Baxter (1991) found that in Australia the nest productivity of three species of

aquatic-feeding ardeids (including Great Egrets) was highest in wet years, with the area of feeding habitat reduced substantially in dry years due to desiccation. Similarly, Rodgers (1987) found that during a five-year period on the west coast of Florida, Little Blue Heron clutch sizes and nestling survivorship declined during years with low rainfall. In all these cases, the common conclusion was that hydrologic trends affected the abundance and/or accessibility of prey, and therefore affected wading bird nest success.

As Frederick and Spalding (1994) suggest, there is little doubt that the availability of prey and nestling provisioning rates are critical proximate determinants of nest success and productivity for many species of wading birds. Powell (1983) and Mock et al. (1987) demonstrated that food-supplemented Great White Herons and Great Egrets raised significantly more young than unsupplemented pairs. Frohring (unpubl. study cited in Frederick and Spalding 1994) demonstrated that the strongest environmental correlate of Snowy Egret and Tricolored Heron nestling growth rates was the density of forage fish in adjacent wetlands. Nonetheless, climatic events, parasites and disease, breeder experience, inter and intra-specific competition for space and nest materials, and predation all may affect egg or nestling survival independent of foraging conditions. Accordingly, exactly how these various factors interact to determine levels of nest success and productivity has been the subject of considerable debate.

In Chapter 2, I documented the patterns of distribution and abundance of foraging wading birds at Lake Okeechobee, Florida, during the nesting seasons of 1989-1992, and examined patterns of habitat selection in relation to vegetative cover types and hydrologic trends. In Chapter 4, I documented trends in wading bird nesting colony establishment, turnover, and composition at the lake, and discussed the

influences of hydrologic and climatic conditions. I summarized trends in annual lakewide nest success and productivity for six species that commonly nest at the lake, and discussed the probable causes of colony and nest failures. In this complementary chapter, I describe a series of logistic regression analyses designed to elucidate associations between the probability of nest failure and a suite of nest-timing, nest-situation, climatic, and hydrologic variables. The six nesting species I studied included: Great Blue Herons, Great Egrets, Snowy Egrets, Tricolored Herons, Little Blue Herons, and White Ibises.

In the regression analyses, I considered only data from 1989-1991, because the nest success data for 1992 were less complete (Chapter 4). Nonetheless, the study period began with high lake stages (>4.5 m NGVD; NGVD = National Geodetic Vertical Datum of 1929, essentially equivalent to height above mean sea level), then spanned a two-year drought that resulted in rapid and large scale declines in the lake stage during the January through August nesting seasons of 1989 and 1990 (10-year low stage in May-June 1990 of 3.2 m NGVD), and then ended with moderate and relatively stable lake stages during the nesting season of 1991. The 1989 and 1991 seasons also featured significant cold weather events that appeared to induce colony abandonments among Great Egrets and Great Blue Herons (Chapter 4). Thus, a wide range of hydrologic and environmental conditions impinged upon the nesting wading birds during the study. Moreover, an examination of data collected at nests revealed that the primary proximate cause of nest failure for all species except perhaps Little Blue Herons was abandonment (Chapter 4). Therefore, I initiated the regression analyses in an effort to elucidate statistically significant associations between the probability of nest failure and environmental variables that may have induced the nest abandonments. I considered two nest situation variables--nest height and overhead cover--in an effort to

account for observed and possible associations with risk of predation, social interactions within colonies, and risks of physical damage due to wind. I considered a date-of-initiation variable to account for consistent seasonal trends that might not be influenced by the climatic and hydrologic variables included in the analyses. I considered a minimum air temperature variable to account for the influence of cold temperatures on foraging efficiency. Finally, I considered various combinations of four hydrologic variables--lake stage, surface-water drying rate, number of days of rising water, and rainfall--calculated over several different time intervals to account for the influence of surface-water hydrology on foraging efficiency.

Study Area and Methods

Study Area

Lake Okeechobee is the third largest freshwater lake in the United States (1,732 km^2 surface area; Herdendorf 1982). The average water depth in the lake is 2.7 m. The lake drains a watershed of nearly 12,000 km^2, primarily through the Kissimmee River from the northwest (Fig. 3-1), and is situated upstream of the remnant Everglades and Florida Bay. The South Florida water Management District (SFWMD) and the US Army Corps of Engineers have primary responsibility for management of the lake stage. A large earthen dike nearly surrounds the lake, and most surface-water inflows and outflows are controlled through canals by hurricane gates, locks, and pumps. However, although human regulation affects the lake stage to a degree, mostly at high stages, the primary factor controlling the lake stage is regional rainfall (Aumen 1994).

The western and southern margins of the lake feature a 400 km^2 expanse of emergent marsh that supports wading bird nesting and foraging activity. The outer littoral zone fringe and bay areas support diverse beds of submerged vegetation that

flourish at lower lake stages (Zimba et al. 1994) and were the focus of concentrated wading bird foraging activity during the 1989 and 1990 drought periods (Chapter 2). The marsh elevation ranges from 3.3 to 4.5 m NGVD, but the elevation is above 4.1 m NGVD in most areas (Richardson and Hamouda 1994). Most of the area to the north and west of the lake has been converted to dairy farms and cattle pastures. Isolated and ephemeral "pocket" wetlands dot the landscape, and pastures are interspersed with sloughs and patches of forested wetland. All of these wetland habitats attracted foraging wading birds sometime during the study, and the floodplains along Fisheating Creek and the Kissimmee River (see Fig. 5-1) also regularly attract foraging birds (Zaffke 1984; McIvor and Smith 1992; unpubl. data). Much of the area south of the lake is covered with sugar cane, rice, and winter vegetable fields, and the myriad canals and ditches that crisscross particularly the sugar cane and rice fields also attract foraging wading birds.

The lake serves as a regional flood-control and water-storage facility of major significance, serving the needs of an extensive agricultural industry and a burgeoning urban population. The lake also supports a multi-million dollar commercial and sport fishing industry, a variety of recreational activities, and a diverse array of game and nongame wildlife species. Aumen (1994) provides a comprehensive overview of the lake ecosystem, and a more detailed account of the natural and management history of the lake.

Nest Monitoring

Each year I selected three to four on-lake nesting colonies for nest success studies (Fig. 5-1; see Table 5-1 for nest sample sizes by colony and year). The sites chosen always included at least two of the largest mixed-species colonies. Additional

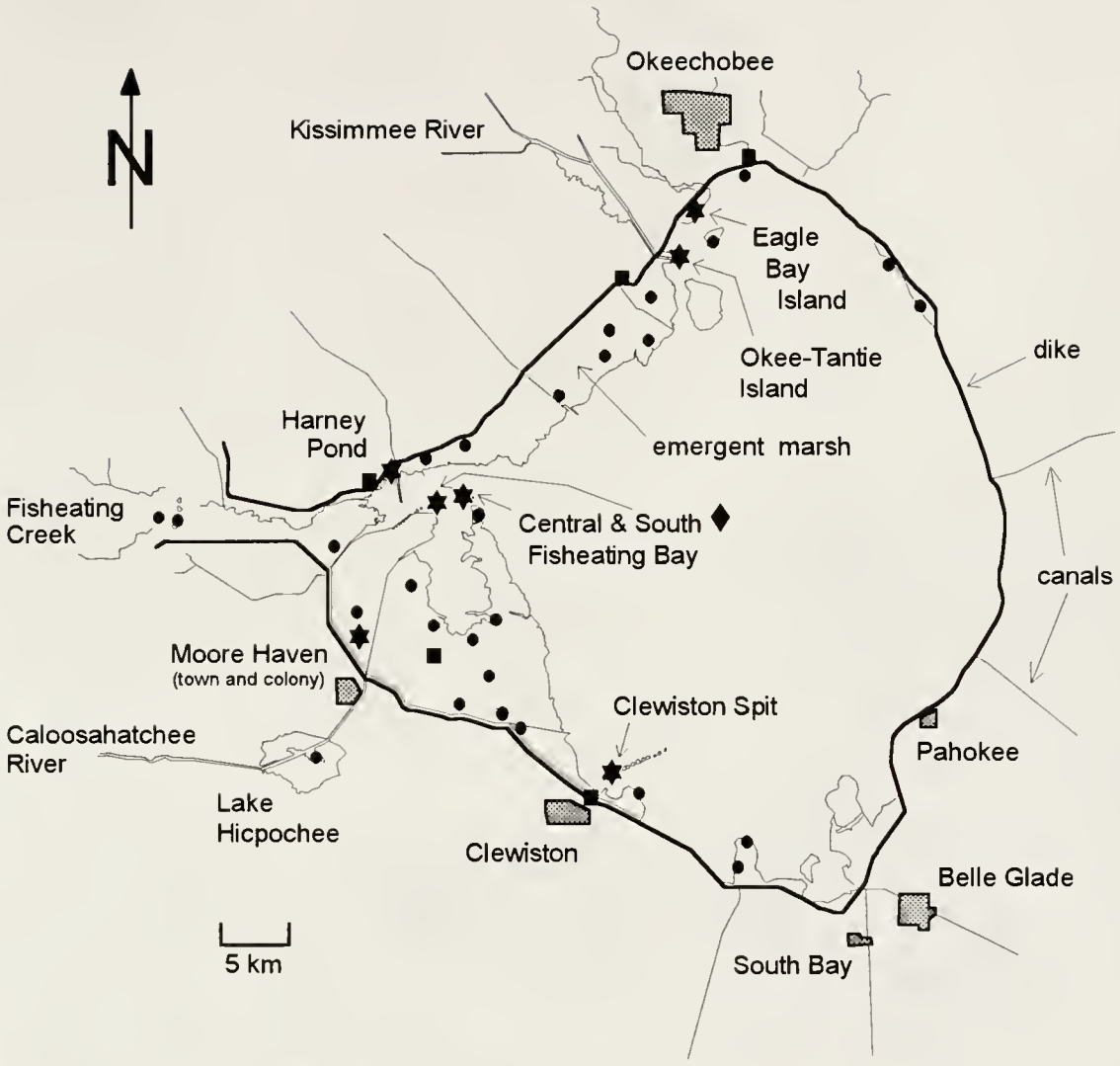


Figure 5-1. Geographic overview of the Lake Okeechobee area showing the locations of nesting colonies and lake stage and rainfall gauging stations.

Table 5-1. Nest sample sizes considered in logistic regression analyses by species, year, and colony.

Year	Colony [a]	Great Blue Heron	Great Egret	Little Blue Heron	White Ibis	Snowy Egret / Tricolored Heron Hatching Model	Snowy Egret Nestling Model	Tricolored Heron Nestling Model
1989	EBI	23 / 18 [b]	19 / 30	12 / 35	6 / 9	12 / 17	0 / 7	5 / 5
	MH	--	19 / 9	5 / 8	19 / 15	74 / 24	40 / 20	10 / 5
	HP	--	2 / 19	--	--	--	--	--
1990	EBI	43 / 20	45 / 43	13 / 8	47 / 37	47 / 10	24 / 2	15 / 6
	CS	--	59 / 24	22 / 8	--	62 / 24	30 / 5	23 / 5
	SFB	--	--	--	--	42 / 5	30 / 4	7 / 1
1991	EBI	0 / 30	26 / 74	4 / 5	38 / 56	48 / 29	11 / 13	19 / 5
	OTI	29 / 8	10 / 30	--	--	--	--	--
	CS	--	69 / 52	--	--	75 / 36	37 / 5	28 / 7
	CFB	--	11 / 3	--	--	39 / 8	23 / 0	15 / 1
TOTALS		95 / 76	260 / 284	56 / 64	110 / 117	399 / 152	195 / 56	122 / 35

[a] EBI - Eagle Bay Island, MH - Moore Haven, HP - Harney Pond, OTI - Okee-Tantie Island, CS - Clewiston Spit, CFB - Central Fisheating Bay, SFB - South Fisheating Bay (see Fig. 5-1 for locations).

[b] Number of successful / failed nests. Failure meant no nestlings were reared to the predefined age threshold (Great Blue Heron - 60 days, White Ibis - 14 days, other species - 21 days), except in the Snowy Egret/Tricolored Heron hatching model where failure meant no eggs hatched.

selections constituted a balance between geographic diversity and adequate species coverage. Great Blue Herons and Little Blue Herons commonly occupied small, isolated, monospecific colonies that I never attempted to visit. Consequently, the nest success data for these species are biased toward those individuals that nested in mixed-species colonies, and I obtained very little data for Little Blue Herons in 1991.

Each year I began marking nests in February, once Great Egrets had begun to lay eggs. Great Blue Herons began nesting in mid-November 1988 and in mid-to-late December in 1990 and 1991 (Chapter 4); the datasets for this species therefore may have underrepresented early failures. In large colonies, I began nest marking excursions at the edge of the colony and continued in a looping pattern into and back out of the center of the concentration of nests to avoid potential edge-effect and nest-density biases. In smaller colonies, I either marked all nests or marked samples of nests throughout the colony. I continued to mark new nests with eggs whenever I discovered them. I revisited each marked nest at 3-8 day intervals until either the nest failed or nestlings reached a predefined age threshold beyond which they became too mobile to census reliably (Great Blue Heron = 60 days, White Ibis = 14 days, others = 21 days; Chapter 4). I continued visits to colonies until the majority of nests in a given colony had either failed or most young had fledged and abandoned the site. I regularly handled and eventually banded all nestlings in many of the accessible marked nests as part of a concurrent study of nestling growth rates (Spalding et al. 1994; unpubl. data).

Datasets and Regression Analyses

The binary response variable in the logistic regression analyses (Hosmer and Lemeshow 1989; SAS Institute Inc. 1990) took the value of one if a nest failed (an "event"), and zero if it was successful. I pooled data from all colonies and years to

maximize the environmental variability represented in the datasets. I focused primarily on datasets where success meant that a nest had produced at least one threshold-age nestling. However, for comparison I also analyzed datasets prepared to investigate the environmental determinants of hatching failure. I will hereafter refer to the regression models used to explain the data when the response was whether or not a fledgling or threshold-age nestling was produced as the "full-cycle" models or analyses, and to those used to explain hatching failures as the "hatching" models.

Snowy Egret, Tricolored Heron, and Little Blue Heron eggs are difficult to distinguish (Hammatt 1981). Therefore, I generally could not identify to species small ardeid nests that failed during incubation. Snowy Egrets and Tricolored Herons usually nested intermixed, but Little Blue Herons typically remained more segregated. In 1989 at one isolated subcolony site on Eagle Bay Island (Fig. 5-1), I was unable to identify 23 nests to species (egg remains indicated 5 hatched). The relative abundance of adults in the area during visits suggested that most of these nests belonged to Little Blue Herons (21 nests hatched, 3 unhatched--adults seen at nest), but Tricolored Herons (5 hatched) and Snowy Egrets (2 unhatched--adults seen) also nested in the area. Otherwise, only six other nests (2 in 1989, 1 in 1990, 3 in 1991) that could have and probably did belong to Little Blue Herons remained unidentified. I therefore felt justified in conducting separate analyses for Little Blue Herons, with the 29 unidentified nests included. For Snowy Egrets and Tricolored Herons, however, I combined data for both species and all unidentified small ardeid nests (including the 29 suspect nests) to develop a hatching-failure analysis. I then also conducted species-specific analyses to elucidate the environmental determinants of post-hatching failure. Henceforth, I will refer to the latter as "nestling" models or analyses to distinguish them from the full-cycle models analyzed for other species.

The independent variables considered in various combinations included: Julian date the first egg was laid (DJUL); height (cm) of the nest above the ground or water surface (NHGT); percent vegetative cover over the nest (NCOV; a subjective visual estimate); mean minimum daily air temperature (°C) during the 14 days prior to nest success/failure (MINT); total rainfall (cm) during the 14, 30, 60, and 90 days prior to success/failure (RAIN14, RAIN30, RAIN60, RAIN90); and three surface-water variables calculated over the same time periods as rainfall. The latter included mean lake stage (STG##, cm NGVD), mean surface-water drying rate (DRAT##, cm day^{-1}), and number of days of rising water (DRIS##).

For nests discovered during laying, I back-estimated the initiation date by assuming a two-day laying interval (Frederick and Collopy 1988). I assigned hatching dates as the mid-point of the preceding visitation interval, unless more definitive data were available (e.g., pipped eggs or nestlings still with matted down). For hatched nests discovered with an apparently complete clutch, I back-estimated the initiation date from the hatch date based on knowledge of each species' typical laying-incubation period (i.e., the average length of time between laying and hatching of the first egg: Great Blue Heron - 28 days, Great Egret - 27 days, White Ibis - 21 days, others - 25 days; Chapter 4). Nests discovered with an apparently complete clutch that failed to hatch presented a more difficult problem. I assigned initiation dates in these cases based on a combination of calculations and empirical evidence. In some cases, I was able to narrow the range of possibilities based on the degree of development evident in dislodged but intact eggs. In addition, many newly built nests were initiated during waves of activity, and therefore it often was reasonable to assign an average date of initiation. Otherwise, I determined the minimum and maximum possible dates and assigned the midpoint of this range as the estimated date of initiation. I identified

"fledging" dates (i.e., the dates when nestlings reached the previously defined threshold ages) based on the assigned hatching dates, and recorded failure dates as the mid-point of the preceding visitation interval if more definitive evidence was lacking.

I obtained rainfall and lake stage data from the SFWMD. The daily lake stage data were collected at one central, open-water station (Fig. 5-1), and I assumed the data represented basin-average conditions (see Chapter 2 for discussion of limitations). Daily rainfall was measured at a variety of gauging stations located primarily around the perimeter of the lake, and I matched data sources to colonies based on proximity (mean distance 4.3 km, maximum 7.3 km). I obtained daily air temperature data from the University of Florida Agricultural Experiment Station located at Belle Glade, just south of the lake, and again assumed the data represented basin-average conditions.

I tested the significance of several different combinations of independent variables in separate regression analyses (Table 5-2). I included DJUL, NHGT, NCOV, and MINT in all preliminary models, except that NCOV was always negligible for Great Blue Herons and Great Egrets and therefore was irrelevant. Otherwise, I ran separate analyses for models that included the 14, 30, and 60-day hydrologic variables, and another for a model that included both 14-day and 90-day variables (hereafter referred to as the 14/90-day model). I assumed that third and higher order interaction terms were of negligible importance, but considered a variety of two-way interactions. These included NHGTxNCOV interactions where appropriate, all two-way interactions involving MINT and the 14, 30, and 60-day hydrologic variables, and all possible two-way interactions between the hydrologic variables except mixed time-interval interactions in the 14/90-day models (Table 5-2).

Table 5-2. Summary of independent variables and models analyzed.

INDEPENDENT VARIABLES

1) Core Variables:

Date-of Initiation (DJUL)
Nest Height (NHGT)
Nest Cover (NCOV) -- irrelevant for Great Blue Herons and Great Egrets
14-day Antecedent Mean Daily Minimum Temperature (MINT)

2) Hydrologic Variables:

Mean Lake Stage (STG##)
Mean Surface-Water Drying Rate (DRAT##)
Number of Days of Rising Water (DRIS##)
Total Rainfall (RAIN##)

⇒ Each calculated over 14, 30, 60, and 90 day intervals antecedent to dates of nest success or failure

3) Interaction Variables:

NHGT x NCOV
MINT x STG## , MINT x DRAT## , MINT x DRAT## , MINT x DRIS##
(no MINT x 90-day hydrologic interactions)
STG## x DRAT## , STG## x DRIS## , STG## x RAIN##
DRAT## x DRIS## , DRAT## x RAIN## , DRIS## x RAIN##
(no mixed 14-day x 90-day hydrologic interactions)

MODELS ANALYZED

1) core variables + 14-day hydrologic variables + interactions
2) core variables + 30-day hydrologic variables + interactions
3) core variables + 60-day hydrologic variables + interactions
4) core variables + 14-day hydrologic variables + 90-day hydrologic variables + interactions

Two sets analyzed for each species:

1) Hatching Models: success = >1 egg hatched
(combined dataset for Tricolored Herons and Snowy Egrets)

2) Full-Cycle Models: success = >1 threshold-age nestling produced
("Nestling" models for Tricolored Herons and Snowy Egrets--hatched nests only)

I generally followed a backward-selection approach for deciding whether to eliminate individual variables. Hosmer and Lemeshow (1989) suggest eliminating variables from further consideration if they fail to achieve a $P < 0.25$ level of significance in univariate models. I discovered, however, that even this "relaxed" α level failed to prevent the elimination of variables that were highly significant when considered in multiple-regression models (i.e., confounding effects were prevalent; Hosmer and Lemeshow 1989: 63-67). Hosmer and Lemeshow also emphasize eliminating main-effects variables that fail to achieve significance in multiple-regression models before considering the importance of interaction terms. Again, my experience suggested that the most fruitful approach was to begin by calculating a model with all main effects and all potentially important interaction terms included before deciding to eliminate any variables. This approach helped guarantee the discovery of complex confounded relationships.

Confounded independent variables (i.e., multicollinearity) can pose problems in regression (Neter et al. 1990: 295-305). In logistic regression, a coefficient represents the estimated log-odds that a unit increase in the independent variable will increase the probability of an event response, if the values of all other independent variables are held constant (Hosmer and Lemeshow 1989: 38-39, 56-58). However, if two independent variables are themselves highly correlated, it is not possible to hold one constant while the other varies, and therefore the meaning of the regression coefficients is less precise (Neter et al. 1990: 300). Accordingly, one must not attempt to interpret the coefficients for one variable without simultaneously considering the relationships indicated for the other. The problem may be eliminated by dropping one or more of the correlated variables, but Neter et al. (1990: 411) note that the magnitude of the coefficients for remaining variables may then change. Hosmer and Lemeshow

(1989: 67) argue that such confounding variables should be retained regardless of their apparent univariate significance. Comparing univariate chi-square (χ^2) statistics might lead to erroneous conclusions, because both variables could appear insignificant when considered together even though each might be significant without the other (Neter et al. 1990: 300).

Another way to assess whether two correlated independent variables are redundant is to compare values of Akaike's Information Criterion (AIC: -2 log likelihood + 2[k + s], with k = number of possible responses, and s = number of explanatory variables in the model; SAS Institute Inc. 1988; Burnham and Anderson 1992) calculated for models with both variables and with one variable eliminated. If the two-variable model scores the lowest AIC (implying a better balance of statistical fit and parsimony), then both variables typically should be retained (cf. Burnham and Anderson 1992). If two or more highly correlated variables are retained, it is particularly imperative that one not use the resulting equations to predict responses based on values of the independent variables outside the range observed during the study (Neter et al. 1990: 300, 411).

I began each model building session by calculating a main-effects-only model for reference. I then forced the inclusion of all main-effects variables while allowing the computer to select among potential interaction terms using the backward-selection method with a significance-level-to-stay (SLS) of 0.25 (SAS Institute Inc. 1990). The SAS program calculates maximum likelihood estimates (MLE's) of the regression coefficients for each of the independent variables, and then computes univariate, adjusted Wald χ^2 statistics for each. The variable with the smallest χ^2 value that does not meet the SLS criteria for remaining is then eliminated from the model, and the process is repeated until all remaining variables satisfy the SLS criteria. After allowing

the computer to select interaction terms in this way, I began a manual selection process to eliminate interaction terms not significant at the 0.05 level while concurrently examining the effect of eliminating insignificant main-effects variables not involved in significant interaction terms. In deciding whether a main-effects variable should be eliminated, I first examined the Wald χ^2 statistic, but also conducted likelihood ratio tests (Hosmer and Lemeshow 1989: 14-15) and compared AIC scores and post-hoc classification efficiencies (SAS Institute Inc. 1990). If these statistics failed to provide unequivocal guidance as to whether a main-effects variable should be eliminated, or if confounding effects were evident, I retained the variable regardless of the Wald χ^2 significance level. Once I repeated this process for each combination of hydrologic variables, I compared AIC, concordance (rank correlation; SAS Institute Inc. 1990), and post-hoc classification statistics for the two sets of four final models, and selected the hatching and full-cycle/nestling model that provided the best balance of statistical fit, parsimony, and interpretability to stand as "reference" models for the species.

Table 5-3 summarizes the variable and reference-model selection and verification processes I went through.

After choosing the reference models, I conducted a series of diagnostic examinations to asses the fit of the models and identify outlier observations (also summarized in Table 5-3). I calculated three summary goodness-of-fit measures. Pearson χ^2 and Deviance (a likelihood ratio test statistic of a saturated model versus the fitted model) statistics are summary measures of the distance between observed and fitted values (i.e., residuals), and therefore help identify the existence of significant

Table 5-3. Summary of variable and reference-model selection and verification processes.

VARIABLE SELECTION

1) Calculate univariate models for each variable and main-effects-only models to use as guides for understanding complex relationships.

2) Automated backward selection beginning with full model (SAS Institute Inc. 1990)

⇒ forced retention of all main effects variables; eliminate non-significant interaction terms with SLS = 0.25

3) Manual, iterative process of elimination and verification:

⇒ verify lack of confounding influences through iterative process of elimination and reentry of both main effects and interaction variables

⇒ eliminate additional interactions not significant at $P \leq 0.05$

⇒ eliminate main effects variables not significant at $P \leq 0.05$
-- if no significant confounding and not involved in significant interaction terms

⇒ significance tests using Wald χ^2 and likelihood ratio χ^2 statistics (SAS Institute Inc. 1990; Hosmer and Lemeshow 1989)

⇒ examination of AIC scores to select combinations of variables that provide best balance of statistical fit and parsimony (SAS Institute Inc. 1990; Burnham and Anderson 1992)

REFERENCE MODEL SELECTION

One model chosen from hatching pool, and one model chosen from full-cycle pool to stand as reference models

Selection criteria in order of importance:

⇒ lowest AIC score (SAS Institute Inc. 1990; Burnham and Anderson 1992)

⇒ highest post-hoc classification efficiencies and estimates of concordance (SAS Institute Inc. 1990; Hosmer and Lemeshow 1989)

⇒ most stable and interpretable, and reflected dominant trends shown in other models

REFERENCE MODEL REGRESSION DIAGNOSTICS

Pearson χ^2, Deviance χ^2, and Hosmer-Lemeshow goodness of fit tests to identify systematic patterns of deviation from optimal fit (Hosmer and Lemeshow 1989)

Graphical analyses to identify outlier observations and observations with unusually high leverage: plots of Δ Pearson χ^2, Δ Deviance χ^2, and confidence interval displacement (C) statistics versus estimated event probabilities (SAS Institute Inc. 1990; Hosmer and Lemeshow 1989)

⇒ test stability of model by eliminating outlier observations and high leverage observations

outliers (Hosmer and Lemeshow 1989). Hosmer and Lemeshow (1989: 140-145) provide another goodness-of-fit test that involves grouping (I used the percentile method) the observations based on estimated probabilities. Significance tests based on the Pearson χ^2 and Deviance statistics may be inaccurate when each observation is associated with a unique set of values (almost always the case when continuous independent variables are involved), and grouping the data overcomes the problem (Hosmer and Lemeshow 1989). Another benefit of the Hosmer-Lemeshow test method is that constructing the test table and calculating the test statistic, $\hat{C}$, helps identify regions of "risk" (i.e., probability regions) where the model does not perform well.

Summary goodness-of-fit measures are a convenient means for assessing how well a model fits the data, but do not identify individual outlier observations. Thus, it is important that one also conducts graphical analyses to examine whether certain individual or small groups of observations are poorly fit by the model or exert undue influence on the structure of the model (Hosmer and Lemeshow 1989). I examined three types of plots to search for such problem observations. The first two involved elements of the Pearson χ^2 and Deviance statistics mentioned above; specifically, $\Delta\chi^2$ and ΔD as described by Hosmer and Lemeshow (1989) and labeled DIFCHISQ and DIFDEV in the SAS LOGISTIC module (SAS Institute Inc. 1990). They are measures of the change in the Pearson χ^2 and Deviance summary statistics that would occur if individual observations were deleted from the dataset. Plotting these statistics against estimated probabilities helps identify individual observations that are poorly fit by the model. The third type of analysis involved plots of the confidence interval displacement diagnostic, C (SAS Institute Inc. 1990), versus the estimated probabilities for each observation. The C diagnostic measures the influence of individual observations on the estimated regression coefficients. It therefore allows one to asses whether individual

observations exert undue influence on the model structure. Observations that are poorly fit by the model and exert a strong influence on parameter estimates should be considered candidates for elimination in the interest of achieving an accurate and stable model (Hosmer and Lemeshow 1989). However, the identification of such observations may also yield important biological insight about unusual cases.

Results

Summary of Nesting Activity and Climatic and Hydrologic Trends

The characteristic rainfall pattern in southern Florida is a late-spring/summer maxima and a late-fall/winter minima (Deuver et al. 1994). During the three years prior to the 1989 nesting season, annual rainfall was high and the lake stage remained above 4.0 m NGVD (I will henceforth drop the NGVD qualifier when referring to stage measurements), but the 1989 nesting season and the beginning of my study coincided with the onset of a two-year drought (see Richardson and Hamouda 1994 for a long-term hydrograph). Great Blue Herons began nesting in mid-November 1988 (Chapter 4), at which time the lake stage was near 4.6 m, but had fallen from a late September high of 4.9 m (Fig. 5-2). By the time Little Blue Herons and White Ibises--the last species to nest--began to build nests in mid-April, the drought had intensified and the lake stage had dropped to 3.9 m. By early August the stage reached a low of 3.4 m. The mean drying rate during the eleven-month recession was -0.46 cm day^{-1}, but several temporary reversals caused by high rainfall interrupted the decline (Fig. 5-2). From early-March through late-April, four multiple-day storms brought colder temperatures, high rainfall, and a reversal in the otherwise prolonged drying trend.

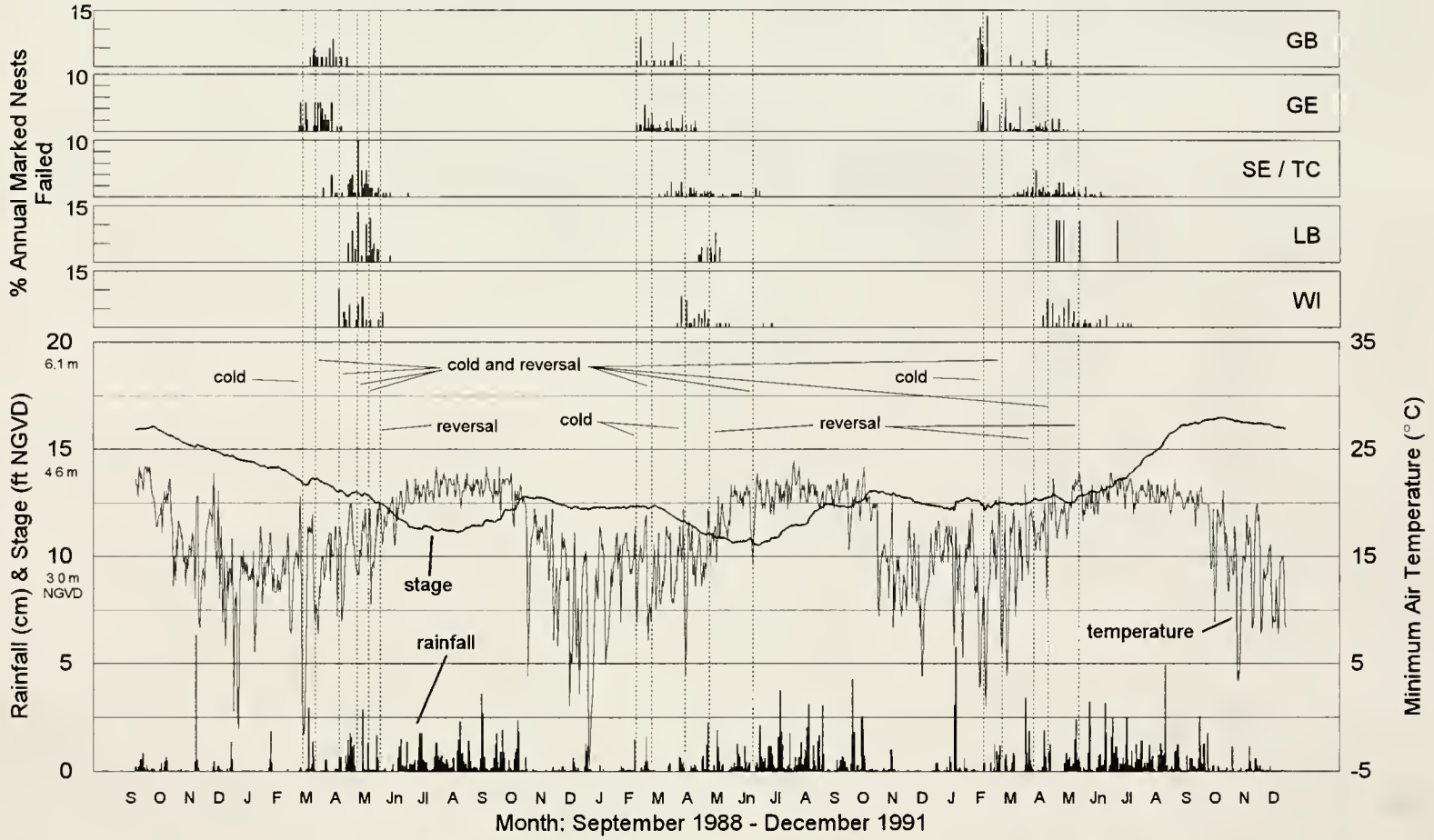


Figure 5-2. Timing of nest failures, 1989-1991, in relation to trends in daily lake stage, rainfall, and minimum air temperature. Dashed vertical lines mark occasions when cold temperatures and reversals in surface-water recessions led to higher nest failure rates. Upper plots indicate the percentages of marked nests--calculated over annual totals--that failed on a given date, and are labelled on the right with species codes: GB = Great Blue Heron; GE = Great Egret; SE / TC = Snowy Egret and Tricolored Heron combined; LB = Little Blue Heron; WI = White Ibis.

Plots of marked-nest failures versus hydrologic and temperature trends provided evidence that nest failure rates increased during and following these events (Fig. 5-2; also see Chapter 4). In May, a relatively steady and rapid recession resumed, and nest failure rates dropped among the species still nesting (i.e., ibises and small ardeids; Fig. 5-2). The recession lasted into July when the summer rainy season began, and all nesting activity ceased by mid-August. The number of nesting attempts or reproductive effort of Great Blue Herons, Great Egrets, and Little Blue Herons was high for the study in 1989, but the nest success of all species was only low to moderate (Chapter 4). Nestling production was also only moderate for most species, but White Ibises and Little Blue Herons were exceptions (Chapter 4). At the height of the 1989 dry season in mid-June, aerial surveys revealed a high estimated total of over 36,000 foraging wading birds on the lake (Chapter 2).

From August through late October 1989, the summer rains brought the lake stage back up, but only to 3.9 m (Fig. 5-2). The lake stage then dropped slightly through December 1989 and then stabilized just above 3.7 m until early March 1990 when a new surface-water recession began. Great Blue Herons did not begin nesting until late December 1989, but all six study species were nesting by mid-March 1990. Both Great Blue Herons and Great Egrets initiated nesting while the lake stage remained stable at late-winter levels, but all other species began nesting shortly after a protracted surface-water recession began in early March. In mid-February, two storm events produced cold temperatures, relatively high rainfall, and a temporary rise in surface-water levels, and Great Blue Heron and Great Egret nest failure rates rose apparently in response (Fig. 5-2). From early March to late April, the lake stage dropped without significant interruption at a very rapid rate of -2.01 cm day^{-1}, but the decline was then interrupted by a 3-day, 2 cm reversal that roughly corresponded to

increases in ibis and small ardeid nest failures. The lake stage then continued to drop unsteadily until late May when an 18-day, 64 cm reversal occurred. The last bout of failures among marked Snowy Egret/Tricolored Heron nests came shortly after the second reversal (Fig. 5-2), which ended with a brief but rapid drop in the lake stage to a 10-year low of 3.2 m. Then the summer rains began in earnest and the lake stage rose unsteadily back up to a 4.0 m by late October. All nesting activity ceased by late August in 1990. The reproductive effort of Great Blue Herons, Great Egrets, and Little Blue Herons was low to moderate, but the reproductive effort of other species was high and the nest success and productivity of all species was high for the study in 1990 (Chapter 4). In mid-June 1990, an estimated total of over 50,000 wading birds concentrated in a relatively small area on the lake (Chapter 2) to feed on dense concentrations of fish and other prey in and between exposed beds of submerged vegetation, primarily Hydrilla (McIvor and Smith 1992; Chick and McIvor 1994).

The lake stage dropped slowly but steadily from October 1990 through January 1991. Great Blue Herons began nesting in mid-December, and Great Egrets began in mid-January. The drying trend, however, did not continue, and in mid-February all the nesting Great Blue Herons and Great Egrets abandoned their effort (Chapter 4). The abandonment occurred following three weeks of fluctuating surface-water levels and toward the end of a 9-day severe but dry cold weather period (minimum daily temperature between 1-12°C, below 5°C on 4 days; Fig. 5-2). Both species eventually initiated second waves of nesting. However, high rainfall precluded the onset of the usual spring surface-water recession, and most species responded with overall low reproductive effort and productivity (Chapter 4). Figure 5-2 again highlights several points in time when cold temperatures and/or rising water trends roughly coincided with periods of nest failure. For most species, the nesting season lasted slightly longer in

1991 than in other years. Both White Ibises and Great Egrets initiated unusually late waves of unsuccessful nests, apparently in response to a brief, but rapid surface-water recession (Chapter 4). The foraging population remained low throughout the 1991 season, with the maximum estimated survey total only 8,450 birds (Chapter 2).

Regression Results

Summaries of the full-cycle and nestling reference models for each species are provided in Table 5-4. The following discussions focus on the findings reflected in these models; however, I relied heavily on information gleaned from the hatching, suboptimal, and non-interaction models to clarify and confirm primary trends, and to highlight important variations associated with the different hydrologic time horizons. I focused my attention on the full-cycle and nestling models, because whether or not a nest succeeds in fledging young is ultimately more important biologically than whether eggs hatch. Nonetheless, it was instructive to compare results for the hatching and full-cycle/nestling models to identify trends that concerned egg security and developed before the parents experienced the high stress of chick rearing. Many species of wading birds probably employ a dynamic and complex array of strategies for responding to changing environmental conditions. The "perfect" model therefore is probably an unrealistic goal. Moreover, I believe it would be unwise to think that a three-year study of a very large system and only spatially coarse-scale environmental data would suffice to identify the "true" model. Thus, for brevity's sake I present detailed results only for the full-cycle and nestling reference models, but in developing my primary conclusions I often blended information from several models.

Table 5-4. Logistic regression models identifying environmental determinants of nest failure for each species.

Species (failed / successful)	Variables [a]	Coefficient	SE	Wald X^2	P	% Correct [b] % Sensitivity [b]	Likelihood Ratio X^2 for Covariates (df: P) $\hat{C}$ [c] (df: *P*)
Great	DJUL	1.918	0.9989	3.69	0.0548	97	225.7
Blue	NHGT	0.073	0.0430	2.90	0.0884	97	(5: 0.0001)
Heron	MINT	-26.190	13.7014	3.65	0.0559		
(76 / 95)	STG90	0.584	0.3257	3.21	0.0732		0.03
	DRIS90	1.783	0.9405	3.59	0.0580		(5: >0.995)
Great	DJUL	1.733	0.4756	13.28	0.0003	98	722.7
Egret	MINT	79.298	28.4770	7.75	0.0054	98	(11: 0.0001)
(284/ 260)	STG60	8.651	2.3790	13.23	0.0003		4.43
	DRAT60	-975.9	452.20	4.66	0.0309		(5: 0.493)
	DRIS60	131.40	36.568	12.90	0.0003		
	RAIN60	12.853	3.4346	14.00	0.0002		
	MINTxSTG	-0.210	0.0750	7.81	0.0052		
	MINTxDRAT	-19.719	5.6371	12.24	0.0005		
	MINTxRAIN	-0.947	0.2494	14.40	0.0001		
	STGxDRAT	3.372	1.2869	6.86	0.0088		
	STGxDRIS	-0.340	0.0947	12.91	0.0003		
Snowy	DJUL	1.101	0.2698	16.65	0.0001	95	219.8
Egret	MINT	-18.212	8.1551	4.99	0.0255	88	(12: 0.0001)
(56 / 195)	STG30	0.096	0.1153	0.70	0.4032		4.27
	DRAT30	500.3	191.20	6.85	0.0089		(5: 0.512)
	DRIS30	53.409	19.6977	7.35	0.0067		
	RAIN30	24.292	6.9334	12.28	0.0005		
	MINTxDRAT	-28.691	11.1612	6.61	0.0102		
	MINTxDRIS	1.436	0.6850	4.40	0.0360		
	MINTxRAIN	-0.699	0.2418	8.36	0.0038		
	STGxDRIS	0.068	0.0208	10.74	0.0010		
	STGxRAIN	-0.038	0.0104	13.25	0.0003		
	DRATxRAIN	0.209	0.0858	5.93	0.0149		

Table 5-4--continued.

Species (failed / successful)	Variables [a]	Coefficient	SE	Wald X^2	P	% Correct [b] % Sensitivity [b]	Likelihood Ratio X^2 for Covariates (df: P) / $\hat{C}$ [c] (df: *P*)
Tricolored	DJUL	0.223	0.0539	17.08	0.0001	90	103.7
Heron	NCOV	-0.023	0.0124	3.59	0.0580	74	(14: 0.0001)
(35 / 122)	MINT	-3.333	0.8183	16.59	0.0001		4.44
	STG14	-0.734	0.2424	9.16	0.0025		(5: 0.493)
	DRAT14	195.40	60.222	10.53	0.0012		
	RAIN14	-19.558	6.1352	10.16	0.0014		
	STG90	0.384	0.1654	5.38	0.0204		
	DRAT90	74.144	41.2880	3.31	0.0688		
	DRIS90	-0.958	0.7433	1.66	0.1974		
	RAIN90	-4.250	1.4555	8.53	0.0035		
	STGxDRAT14	-0.502	0.1556	10.40	0.0013		
	STGxRAIN14	0.051	0.0159	10.42	0.0012		
	DRATxRAIN90	-4.397	1.7810	6.09	0.0136		
	DRISxRAIN90	0.097	0.0354	7.50	0.0062		
Little	DJUL	0.916	0.3921	5.46	0.0195	93	148.8
Blue	NHGT	-0.082	0.0409	4.04	0.0445	94	(7: 0.0001)
Heron	MINT	-7.619	3.7309	4.17	0.0411		0.56
(64 / 56)	DRAT30	74.700	35.8066	4.35	0.0370		(5: 0.988)
	RAIN30	10.282	5.0555	4.14	0.0420		
	MINTxDRAT	-3.114	1.6367	3.62	0.0571		
	MINTxRAIN	-0.634	0.3059	4.30	0.0381		
White	DJUL	2.196	0.8498	6.67	0.0098	94	290.6
Ibis	NHGT	-0.087	0.0341	6.47	0.0110	94	(11: 0.0001)
(117 / 110)	MINT	172.70	65.345	6.99	0.0082		0.42
	STG14	9.276	3.4567	7.20	0.0073		(4: 0.981)
	STG90	-3.478	1.5209	5.23	0.0222		
	DRAT90	2306.9	972.90	5.62	0.0177		
	RAIN90	-27.126	12.4294	4.76	0.0291		
	MINTxSTG14	-0.530	0.2005	6.99	0.0082		
	STGxDRAT90	-6.110	2.5779	5.61	0.0178		
	STGxRAIN90	0.070	0.0325	4.61	0.0318		
	DRATxRAIN90	8.981	3.6676	6.00	0.0143		

Table 5-4--continued.

Note: Data from 1989-1991 were pooled. See text and Tables 5-2 and 5-3 for details on variable and model selection methods.

[a] Variables: DJUL = Julian date first egg laid; NHGT = nest height (cm); NCOV = percent vegetative cover over nest; MINT = mean minimum daily air temperature (°C) 14 days prior to success/fail; and hydrologic variables representing different antecedent time periods--STG## = mean lake stage (cm NGVD), DRAT## = mean drying rate (cm/day), DRIS## = days of rising water, and RAIN## = total rainfall (cm). All two-way interactions of MINT and the hydrologic variables and between hydrologic variables, and NHGTxNCOV terms were considered, except that no mixed time-horizon interactions were analyzed in 14/90-day models. Variables generally were eliminated from final models if the univariate Wald X^2 failed to reach a $P \leq 0.05$ level of significance, but see text for details.

[a] Post-hoc classification efficiencies calculated by the SAS LOGISTIC procedure (SAS Institute Inc. 1990): % correct = percent of all observations classified correctly; % sensitivity = percent of events (i.e. failures) classified correctly.

[c] Hosmer-Lemeshow (1989: 140-145) goodness-of-fit statistic.

General trends. Every multiple-regression model indicated that both date-of-initiation (DJUL) and minimum air temperature (MINT) were significant determinants of nest failure (e.g., see Table 5-4). The significance of DJUL often depended on MINT being included, but the opposite usually was not true. A positive correlation between the two variables (Pearson r = 0.46-0.77, depending on species) confirmed that the average temperature increased as the season progressed (also see Fig. 5-2). Considered alone in univariate models, MINT was a highly significant (likelihood ratio χ^2 $P \leq 0.007$) negative determinant of nest failure in all cases except the hatching model for Little Blue Herons (P = 0.153, positive relationship). Thus, failure rates usually increased during cold weather periods, which my field observations confirmed for Great Blue Herons and Great Egrets (Chapter 4). DJUL was also highly significant ($P \leq$ 0.003) in the univariate hatching and full-cycle models for Great Blue Herons and in the

univariate hatching model for Little Blue Herons (P = 0.002), and was only marginally significant but fell under the P = 0.25 cutoff in the Great Egret univariate hatching model and in the Little Blue Heron and Snowy Egret univariate full-cycle/nestling models. However, in the five remaining cases, the univariate P values for DJUL ranged from 0.596 to 0.838, yet DJUL contributed significantly to all multiple-regression models in which MINT was included. Moreover, the relationship between DJUL and the probability of nest failure was always positive, while the relationship between MINT and failure was generally negative (often complicated by significant interactions). This implied that, with MINT included to account for early losses during late-winter cold fronts and with other primary climatic and hydrologic influences also accounted for, late-season nests failed significantly more often than early nests among all species.

All the final hatching and full-cycle/nestling models, for all species, accounted for highly significant proportions of the variance in each dataset (likelihood ratio χ^2 test for covariates, $P < 0.0001$).

Great Blue Herons. None of the applicable two-way interaction terms significantly improved the Great Blue Heron full-cycle models; interpreting the regression coefficients therefore was simple. Moreover, the best-fit full-cycle model arose from the 14/90-day combination of hydrologic variables, but all the 14-day variables (not including the 14-day MINT variable) were insignificant. The final model contained only the 90-day stage (STG90) and days-of-rising-water (DRIS90) variables, along with DJUL, nest height (NHGT), and MINT terms (Table 5-4). The 60-day model--with an analogous structure--ranked second best (60-day AIC = 27.5, 30-day AIC = 21.3). Table 5-5 lists means and ranges for each of the variables retained in the full-cycle reference model.

Table 5-5. Means and ranges of independent variables included in the full-cycle or nestling models for each species.

Species	Variable[a]	Mean	Minimum	Maximum
Great Blue Heron	DJUL	36	-29	96
	MINT	14.7	8.5	21.3
	NHGT	291	61	483
	STG90	385	348	433
	DRIS90	27	10	51
Great Egret	DJUL	60	13	114
	MINT	14.6	8.5	21.4
	STG60	384	355	428
	DRAT60	-0.13	-0.68	0.20
	DRIS60	21	4	34
	RAIN60	12.3	3.7	32.5
Snowy Egret	DJUL	98	66	146
	MINT	18.3	14.2	21.4
	STG30	368	325	398
	DRAT30	-0.21	-1.02	0.55
	DRIS30	10	1	21
	RAIN30	11.1	1.6	18.6
Tricolored Heron	DJUL	95.9	69	139
	NCOV	57	0	100
	MINT	18.3	13.6	21.4
	STG14	368.6	325	401
	DRAT14	-0.15	-1.11	0.83
	RAIN14	5.0	0	14.7
	STG90	376	332	406
	DRAT90	-0.19	-0.65	0.25
	DRIS90	31	11	51
	RAIN90	23.1	9.7	44.7
Little Blue Heron	DJUL	105	80	162
	NHGT	132	41	221
	MINT	17.5	14.2	21.8
	DRAT30	-0.41	-1.01	0.65
	RAIN30	8.3	1.1	18.4
White Ibis	DJUL	114	87	186
	NHGT	131	30	264
	MINT	18.2	13.3	21.9
	STG14	371	324	423
	STG90	379	331	416
	DRAT90	-0.18	-0.58	0.40
	RAIN90	19.2	6.1	33.9

[a] See Table 5-2 or text for variable descriptions. DJUL is Julian date number; MINT in °C; NCOV is percentage; NHGT, STG##, and RAIN## in cm; DRAT## in cm day^{-1}; DRIS## in days.

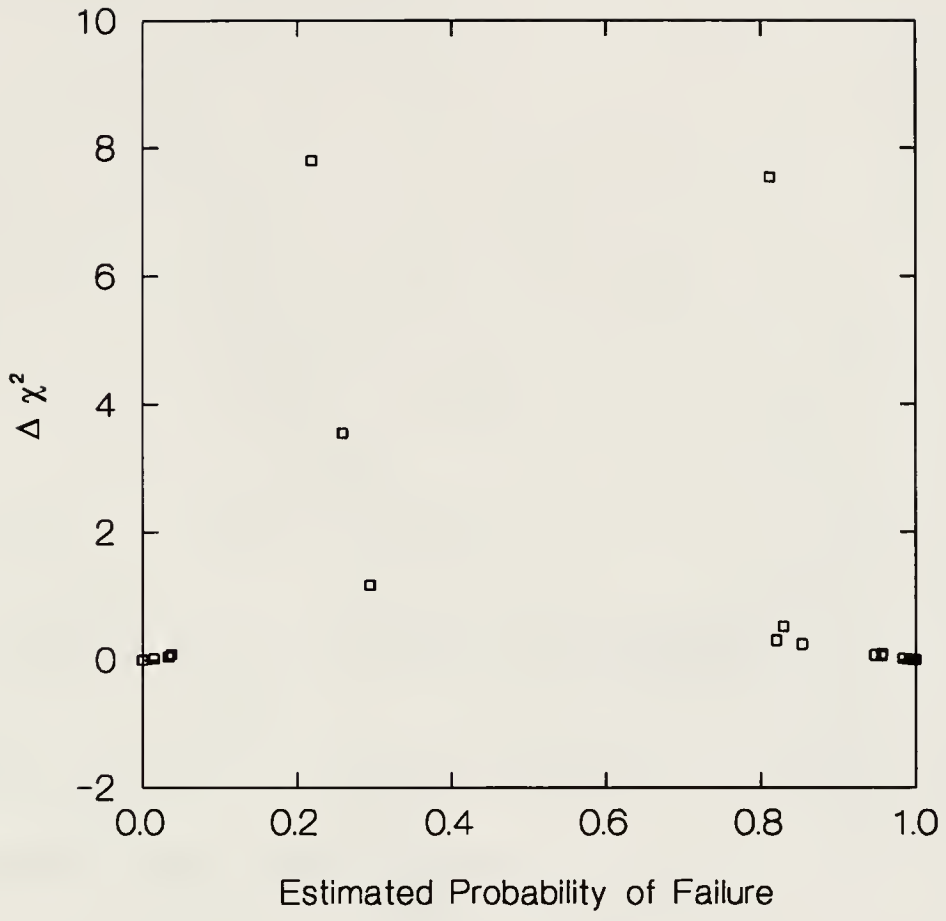
Besides reflecting the influence of DJUL as mentioned above, the full-cycle reference model (Table 5-4) confirmed that the probability of nest failure: 1) increased as MINT dropped; 2) increased as nest height increased; 3) increased when the 90-day mean lake stage was high; and 4) increased during periods of rising surface water (consult Table 5-5 for implications of relative terms). The drying rate variable DRAT90 could be substituted for DRIS90, but the AIC for the resulting model was higher than for the model with DRIS90 (31.7 versus 21.2), and the post-hoc classification efficiency was slightly lower (overall correct - 94 versus 97%; sensitivity - 96 versus 97%). This suggested that the magnitude of change in mean water depths was less important than the consistency of trends. The final 30-day full-cycle model indicated similar trends, but also suggested that high or at least consistent rainfall decreased the chance of failure. However, rainfall variables were no where near significant in any other full-cycle model.

The Wald χ^2 statistics shown in Table 5-4 suggest that all the variables were only marginally significant in the full-cycle reference model. However, if NHGT is dropped from the model, all the remaining variables are rated highly significant ($P < 0.004$), but the AIC score increases from 21.2 to 31.4, which is an unacceptably large increase (cf. Burnham and Anderson 1992). Moreover, a likelihood ratio test of the significance of NHGT indicated a highly significant contribution ($\chi^2 = 12.14$, df = 1, $P < 0.001$). I therefore left NHGT in the model despite the misleading Wald χ^2 significance levels.

The hatching models revealed similar trends, but a more complex set of relationships. NHGT did not contribute significantly to any of the hatching models. The best-fit model included both 14 and 90-day STG and DRIS variables, DJUL, MINT, RAIN90, and MINTxDRIS14 and DRISxRAIN90 interaction terms. The coefficients for the MINT and MINTxDRIS14 terms indicated that although under most circumstances a

decrease in temperature increased the probability of nest failure, an increase in temperature increased the probability of failure if the lake stage was dropping steadily (low DRIS14). Similarly, rising water increased the probability of failure over the short term, except when the temperature remained above average. The coefficients for DRIS90 and RAIN90, and the DRISxRAIN90 interaction further confirmed that constantly rising water due to high rainfall increased the probability of failure, but that otherwise relatively high--probably consistent--long-term rainfall decreased the probability of failure. The relationship with failure was positive for STG14, but negative for STG90. This suggested that high water during the nesting season increased the probability of nest failure, but that a high winter lake stage decreased the probability of failure.

The Great Blue Heron full-cycle reference model ranked high in terms of post-hoc classification efficiency (97% of all observations and 97% of failures classified correctly), and the Hosmer-Lemeshow goodness-of-fit statistic confirmed a very good fit ($P > 0.995$; Table 5-4). Plots of $\Delta\chi^2$ and ΔD versus predicted probabilities confirmed that only two observations were not well accounted for by the model ($\Delta\chi^2 = 6.6$ and 7.3; Fig. 5-3 shows the $\Delta\chi^2$ plot to provide an illustrative example of one such plot). One of these observations was an unusual early failure, while the other was a late success for the year and colony involved. Despite apparently accounting for additional subtleties, the best hatching model was overall less efficient than the best full-cycle model (94% of all observations and 84% of failures classified correctly), and the Hosmer-Lemeshow statistic confirmed a slightly poorer, but still very good fit ($\hat{C} = 1.958$, df = 4, $P = 0.774$). In this case, one observation was very poorly fit by the model--a failure probably due to



Pearson χ^2 = 9.5 df = 165 P > 0.995

Note: lower points represent many individual nests.

Figure 5-3. Example of Δ Pearson χ^2 regression diagnostics plot for the Great Blue Heron full-cycle model.

infertile eggs ($\Delta\chi^2$ = 485); however, deleting the observation did not appreciably alter the structure of the model or the coefficient values, so I retained it.

To summarize, the probability of Great Blue Heron nest failure increased when:

- nests were initiated late in the season
- nest height was high
- the minimum daily air temperature dropped
  - high temperatures increased the probability of failure at the height of the drought when the surface-water level was decreasing steadily
- the mean lake stage was high
  - a high winter lake stage decreased the probability of failure, but high water during the nesting season generally increased the probability of failure
- the lake stage was rising steadily
  - an increasing lake stage or at least less consistent drying decreased the probability of failure if temperatures remained high and long-term rainfall was low
- long-term rainfall was low
  - the relationship was significant only in the hatching models, and high rainfall increased the probability of failure if it led to constantly rising water

Great Egrets. The 60-day hydrologic variables provided the most discriminatory power among the full-cycle models (Table 5-4). The 14/90-day model ranked second best, but the AIC score was markedly higher (109.5 versus 54.3 for the 60-day model). All the Great Egret models indicated the typical influence of DJUL and a highly

significant association with MINT. All four 60-day hydrologic variables contributed significantly to the full-cycle reference model, and five interaction terms were also highly significant (Table 5-4). Table 5-5 lists means and ranges for all the variables retained in the full-cycle reference model.

When considered in multiple-regression models, NHGT never rated as a significant determinant of nest failure for Great Egrets, but rated highly significant when considered alone in both the hatching and full-cycle univariate models ($P = 0.008$). The univariate relationship with failure was negative, suggesting that low nests failed more often (NHGT range 71-462, mean 193 cm). The discrepancy meant that either the trend in the data explained by nest height paled in importance when compared to trends accounted for by other variables, or that nest height only weakly accounted for a trend better explained by another variable(s) in the multiple-regression context. In the full-cycle dataset, NHGT was most strongly correlated with the longer-term rainfall variables (Pearson $r = +0.51$-0.54). High long-term rainfall may have resulted in healthier and taller vegetation, which may in turn have allowed nests to be built higher up in the canopy. Relatively high or at least consistent long-term rainfall was generally associated with low nest failure; perhaps higher success among nests built higher in the vegetation was a simple coincidence due to the rainfall effect on vegetation.

As was true for Great Blue Herons, all the Great Egret models indicated that the probability of nest failure usually increased as MINT dropped. However, unlike for Great Blue Herons, all the final Great Egret models included significant MINT interaction terms (e.g., see Table 5-4). Table 5-6 illustrates the process I went through to arrive at conclusions when interaction terms were involved, using the relationships for MINT as the example. I calculated ranges of possible values (based on data in Table 5-5) for each term in the predictive equation representing the influence of the

Table 5-6. Example of procedure for interpreting relationships when several interactions involved; example is for interpreting effects of minimum temperature on Great Egret nest success based on full-cycle model.

Term	Calculation Factors	Minimum Value	Mean Value	Maximum Value
MINT	79.30	+79.3	+79.3	+79.3
MINT x STG60	-0.21 * STG60	-89.9	-80.7	-74.6
MINT x DRAT60	-19.72 * DRAT60	-3.9	+2.6	+13.4
MINT x RAIN60	-0.95 * RAIN60	-30.9	-11.7	-3.5
	Totals	-45.4	-10.5	14.6

Implications: combined total negative--indicating negative association between MINT and nest failure--except when 60-day mean lake stage low (low STG60), 60-day drying rate high (high negative DRAT60), **and** 60-day rainfall low (low RAIN60);

⇒ a drop in temperature usually increased the probability of nest failure, especially when rainfall was high and the lake stage was high and rising rapidly;

⇒ however, during peak drought periods, an increase in temperature increased the probability of failure.

main-effects variable in question. I then determined which combinations of plausible values resulted in overall negative and positive sums; i.e., under which sets of conditions did an increase in the main-effect variable lead to increased nest failure, and under which conditions was the opposite true. In this case, the combination of coefficients for the MINT, MINTxSTG60, MINTxDRAT60, and MINTxRAIN60 terms in the Great Egret full-cycle reference model indicated that a drop in the mean minimum daily temperature usually increased the probability of failure, especially when rainfall was high and the lake stage was high and rising. However, an increase in temperature increased the probability of failure at low lake stages following prolonged drying when rainfall remained scarce (i.e., during peak drought periods). The best-alternative 14/90-

day model suggested that high temperatures might also increase the chance of failure when combined with constantly rising surface-water levels (i.e., high DRIS14).

The coefficients for the STG60, STGxDRAT, and STGxDRIS terms in the full-cycle reference model (Table 5-4) indicated that a higher mean stage increased the probability of failure unless combined with steadily but slowly rising water (high DRIS60, but low positive DRAT60) or high temperatures and rapid drying. The coefficients for RAIN60 and the MINTxRAIN interaction term indicated that--with surface-water trends accounted for by other variables--high or at least consistent rainfall decreased the probability of failure for nesting Great Egrets, unless MINT was below average (i.e., cold, rainy weather increased the probability of failure).

Contrary to the case for Great Blue Herons, both DRAT and DRIS variables were retained in most of the final Great Egret models. The DRIS60 and DRAT60 terms--and the related interaction terms--accounted for unique trends in the full-cycle reference model (Table 5-4), despite the fact that the two variables were themselves highly and positively correlated ($r = 0.97$). One might initially suppose that two variables correlated to such a high degree would reflect largely redundant information. However, AIC scores, levels of confounding, and other goodness-of-fit statistics indicated that including both DRAT and DRIS greatly improved the discriminatory power of several models. Including both variables often allowed the models to account for distinct relationships that a single variable could not have accounted for simultaneously (except that higher-order polynomial terms might have accomplished the same thing). Moreover, the two variables often counter-balanced the effect of one another, indicating that both the magnitude (DRAT) and regularity (DRIS) of changes in surface-water levels affected nesting birds. Great Egrets usually fared best when the surface-water level was receding rapidly (negative DRAT60), except at the height of the drought

when the mean depth was low and temperatures were high. Conversely, an increase in the number of days of rising water increased the probability of failure if the lake stage was below average, but decreased the probability of failure if the lake stage was above average. In combination with data for STG60, these results suggested that the probability of nest failure decreased most in conjunction with lower lake stages and rapidly and steadily receding surface-water levels (i.e., the mid-1989 and 1990 scenarios; see Fig. 5-2). However, a slower drying rate--probably not rising water--decreased the probability of failure at very low lake stages when temperatures remained high (i.e., late in the 1990 nesting season), and steadily but slowly rising water did not increase nest failure at higher lake stages (i.e., conditions that pertained in 1991).

The 30-day hydrologic variables provided the most discriminatory power among the Great Egret hatching models; the 14/90-day set again ranked second best. The 30-day reference model, 14-day, and 14/90-day hatching model results for MINT emphasized--as did the 14/90-day full-cycle model--that high temperatures increased the probability of failure when the lake stage was high and surface-water levels rose abruptly (positive DRAT but low DRIS). The coefficients for and interactions among the four hydrologic variables further emphasized that Great Egrets fared best at lower lake stages when water levels were receding, but also indicated that the combination of a slow, steady rising trend and high stages did not increase the probability of nest failure. The results for rainfall variables also confirmed that periodic rainfall decreased the probability of failure at very low lake stages during the drought.

The Great Egret full-cycle reference model ranked slightly higher than the best Great Blue Heron model in terms of post-hoc classification efficiencies (98 versus 97%), but the Hosmer-Lemeshow goodness-of-fit statistic indicated greater deviation

from an optimal fit (P = 0.493 versus >0.995; Table 5-4). Plots of residuals revealed two nests that were strong outliers ($\Delta\chi^2$ = 21.2 and 25.3) and four that were moderate outliers ($\Delta\chi^2$ = 3.9-8.4). One of the strong outlier nests was unusual because it failed with relatively old nestlings (18 days), for unknown reasons. The other was unusual because it was the latest of the successful nests. Deleting the observations, however, again did not greatly affect the structure of the model. The more moderate outlier nests may all have failed due to predation, a fate that the independent variables could not directly account for. The best Great Egret hatching model again achieved a lower overall efficiency than the best full-cycle model (86 versus 98% classified correctly, 83 versus 98% sensitivity). The Hosmer-Lemeshow statistic indicated a less systematic pattern of deviation from an optimal fit in the hatching model ($\hat{C}$ = 6.641, df = 8, P = 0.573), but residual plots for the hatching model indicated that a greater number of nests were associated with moderate to large residuals than was true in the full-cycle model. Most of the outlier nests were failures, and many failed around hatching time. The sudden disappearance of whole clutches after a lengthy incubation period suggested failure due to predation. I did not confirm hatching in any of these cases, but newly hatched nestlings, rather than eggs, may have been the target of the predators (e.g., Black-crowned Night Herons).

To summarize, the probability of Great Egret nest failure increased when:

- nests were initiated late in the season
- the minimum daily air temperature dropped
  - high temperatures increased the probability of failure following prolonged drying at low lake stages with low rainfall, and probably also during abrupt reversals to rising water, especially at higher lake stages

- the mean lake stage was high
  - unless accompanied by a slow, steady rising-water trend
  - very low lake stages increased the probability of failure following prolonged drying if temperatures remained high and rainfall low
- the lake stage was increasing
  - a slower drying rate decreased the probability of failure at low lake stages when temperatures remained high and rainfall low, and a slow, steady rising-water trend did not increase the probability of failure at high lake stages
- rainfall remained low for extended periods
  - high rainfall increased the probability of failure if combined with cold temperatures or if it led to a rapid rising-water trend, particularly if the transition to rising water was abrupt

Snowy Egrets and Tricolored Herons. The 14/90-day mix of hydrologic variables provided the most discriminatory power among the combined-species hatching models, and outperformed the best-alternative 60-day hatching model by a large margin (60-day AIC = 491.9, 14/90-day AIC = 432.7). The 14/90-day variables were also the most effective for discriminating Tricolored Heron nestling-period failures (Table 5-4; 14/90-day AIC = 92.9, best-alternative 60-day model AIC = 105.6), but the 30-day variables were most effective for Snowy Egrets (Table 5-4; 30-day AIC = 72.6, best-alternative 14/90-day model AIC = 97.2). All models indicated a highly significant relationship for DJUL. Table 5-5 lists means and ranges for all variables retained in the nestling models for both species.

All of the combined-species hatching models indicated that the probability of nest failure increased as nest height increased (NHGT range 48-315, mean 139 cm);

however, although the relationship was significant according to the final 14, 30, and 60-day models and the univariate model ($P < 0.023$), it was only marginally significant in the 14/90-day reference model ($P = 0.095$). Comparisons of AIC scores and post-hoc classification efficiencies, and a likelihood ratio test confirmed that the NHGT variable added little to the reference model. Nonetheless, although it was clear that climatic and hydrologic variables were more important determinants of nest success, the fact that nest height was significant in all models except the reference model suggested that a high nest increased the probability of failure for at least some nesting pairs of one or both species. Height effects were much less prevalent in the nestling models, but NHGT was closest to significant in the best nestling models for both species ($P = 0.08$-0.09) and was significant according to the Snowy Egret univariate model ($P = 0.034$). The relationship with failure, however, was negative in the nestling models rather than positive as in the hatching models.

The contribution of the nest cover variable (NCOV) was unequivocally significant only in the least efficient of the Tricolored Heron nestling models. However, I included the NCOV variable in the reference model version shown in Table 5-4 because, although the Wald χ^2 statistic did not quite reach the 0.05 level of significance ($P = 0.058$), the likelihood ratio χ^2 statistic did ($\chi^2 = 4.033$, df = 1, $P = 0.046$). Moreover, the AIC score for the model with NCOV was slightly lower (92.9 versus 94.9), and including NCOV accounted for the correct classification of two additional failures (6% of the total). The coefficient for NCOV was negative, indicating that high cover decreased the probability of failure for some Tricolored Herons with nestlings. NCOV never approached significance as a determinant of nest failure for Snowy Egrets with nestlings.

As for previous species, all models indicated that the probability of nest failure increased significantly among Snowy Egrets and Tricolored Herons when temperatures dropped. The same exceptions shown for Great Egrets also applied. Only one interaction was significant in the combined-species hatching reference model, MINTxSTG14, and this indicated that high temperatures increased the probability of failure at minimum lake stages. The second-best 60-day version indicated that high temperatures increased the probability of failure if the surface-water level had been dropping steadily (minimum DRIS60; i.e., a drought effect), but also if the lake stage and rainfall were very high (i.e., the combination of high temperatures and rapidly rising water at high stages increased the probability of failure). The Snowy Egret nestling model confirmed the same drought-related exception (i.e., high temperatures increased the probability of failure if combined with rapid drying and low rainfall), and included an opposite interaction with DRIS30 (Table 5-4). The latter complexity suggested that abrupt, rapid drops in the surface-water level (strongly negative DRAT, but higher DRIS) increased the probability of failure during drought periods if combined with high temperatures, but that the combination of high temperatures and constantly rising water also increased the probability of failure. No MINT interaction terms contributed significantly to the Tricolored Heron nestling reference model (Table 5-4), but the second-best 60-day model confirmed the same drought and rising-water exceptions.

The combined-species hatching reference model indicated that a short-term increase in the mean stage (STG14) increased the probability of failure, more so if the water-level was rising steadily (high DRIS14), but less so if temperatures were high (i.e., during the drought). In contrast, the model indicated a simple negative relationship between the probability of failure and STG90. This suggested the same scenario demonstrated in the hatching models for Great Blue Herons; i.e., high surface-

water levels generally increased the probability of failure during the nesting season, but high winter stages improved the chances of nest success. The results for DRIS14 showed that a short-term increase in the number of days of rising water decreased the probability of failure only when the lake stage and rainfall were low. The results for the long-term DRIS90 and DRAT90 variables indicated that a decrease in the drying rate always increased the probability of failure. However, the response was less pronounced if the surface-water level had already been fluctuating (higher DRIS90), and a slow, steady rising trend did not increase the probability of failure. Significant RAIN14 and RAINxDRIS14 terms showed that high short-term rainfall usually increased the probability of nest failure, especially if it contributed to a constant rising-water trend. In contrast, a significant negative relationship between failure and RAIN90 showed that consistent long-term rainfall decreased the probability of failure.

The Snowy Egret nestling reference model emphasized that the combination of a high lake stage and constantly rising water increased the probability of nest failure, particularly if temperatures were also high (Table 5-4). The results for DRAT30 and the MINTxDRAT30 interaction term suggested that at least a slower drying rate, if not rising water, decreased the probability of failure unless the temperature remained low; however, all other models emphasized that an increase in DRAT increased the probability of failure, especially if DRIS was also high. Variations evident in the different models suggested that a slower drying rate improved nest success if the lake stage was high and temperatures remained high, but a rapid drying rate improved nest success once the stage had dropped to more moderate levels or if temperatures remained low. The reference model also showed that high rainfall increased the probability of failure if it caused a rising-water trend, particularly if the temperature or lake stage was low. However, an increase in rainfall decreased the probability of failure

if the temperature and lake stage were above average and a constant rising-water trend did not result. Other models further emphasized that reversals in otherwise prolonged drying trends due to high rainfall increased the probability of failure particularly at lower lake stages.

The hydrologic trends indicated in the Tricolored Heron nestling models were similar in gross detail to those shown for Snowy Egrets (Table 5-4). A high mean lake stage increased the probability of failure over the long-term, but a higher short-term mean stage decreased the probability of failure unless the surface-water level was dropping rapidly or if high rainfall led to a rising-water trend. The results for DRAT14 emphasized that over the short term--i.e., during the nesting season--a slower drying rate improved the chance of success if the stage was high, but otherwise a rapid drying rate was associated with low nest failure. However, the results for DRAT90 and DRIS90 indicated that over the long term a slower drying rate--but not rising water--decreased the probability of failure. Interactions with the long-term RAIN90 variable emphasized that a constant rising-water trend due to high rainfall increased the probability of failure, and the results for RAIN90 itself emphasized that an abrupt and prolonged reversal of an established drying trend increased the probability of failure. Otherwise, relatively high long-term rainfall decreased the probability of failure, suggesting that consistent but probably not high rainfall was important to survival during the drought.

The Snowy Egret and Tricolored Heron models were the least efficient in terms of post-hoc classification sensitivity, and the combined-species hatching model rated considerably lower than either species' nestling model (60% versus 74% for Tricolored Herons and 88% for Snowy Egrets). The overall classification efficiency was higher in all cases (86-95%), but as Hosmer and Lemeshow (1989: 147) note, such post-hoc

procedures usually favor classification into the larger of the component groups--in these cases the non-event or success group (Table 5-4). The Hosmer-Lemeshow goodness-of-fit statistics for the two nestling models indicated a good fit, comparable to that shown for the Great Egret full-cycle model (Table 5-4). Residual plots for the Snowy Egret model at first revealed one extreme outlier nest that exerted great leverage on the structure of the model. Although I detected no obvious biological reason for the nest to be so much of an outlier, I decided to eliminate the nest to achieve a more stable model. Subsequent residual plots revealed three additional outlier nests ($\Delta\chi^2$ = 10.9, 34.7, and 111.0); deleting these observations improved the fit of the model, but did not markedly affect the model structure or the estimated coefficients, so I did not eliminate them from the dataset. All three nests were unusual in that they appeared to fail with fairly large nestlings (12-16 days). Resident alligators may have consumed one brood, but the others might simply have relocated away from the original nest site. Four nests--all failures--were noticeable outliers in the Tricolored Heron nestling dataset ($\Delta\chi^2$ = 10.8-36.8), but again there was no sound reason for eliminating them. One nest was unusual because it appeared to fail with two 18-19-day nestlings, and was one of the earliest recorded failures. I found one of the nestlings dead under the nest, but the other may have relocated and survived. The nestlings in another of the suspect nests may have died due to disease. A night-heron may have preyed upon another brood just after the nestlings hatched. The last nest was unusual because it was initiated very late.

Unlike for the nestling models, the Hosmer-Lemeshow test for the combined-species hatching model indicated a significant pattern of deviation from an optimal fit ($\hat{C}$ = 15.597, df = 8, P = 0.049). Closer scrutiny of the distributions of observed responses and predicted probabilities revealed a poor fit across all but the most

extreme deciles of risk (sensu Hosmer and Lemeshow 1989). This showed that there was a wide range of covariate patterns not adequately accounted for by the model, as opposed to there being a specific, identifiable set of environmental conditions and associated responses that the model did not account for. The logical conclusion was that combining data for the two species obscured divergent, species-specific trends and thereby resulted in a poorly fitted model. Nonetheless, the hatching-model structure did reflect some trends evident in both species nestling models, and the results for nest height conformed to expectations based on field observations (see discussion section).

To summarize, the probability of Snowy Egret hatched-nest failure increased when:

- nests were initiated late in the season
- nest height was low
  - the effect was only marginally significant, and a high nest may have increased the probability of failure for some pairs during incubation
- the minimum daily air temperature dropped
  - high temperatures increased the probability of failure if combined with rapid drying and low rainfall, or if combined with continually rising water
- the long-term mean lake stage was high
  - over the short term a higher stage decreased the probability of failure if water levels remained stable
- the lake stage was increasing

  - a slower long-term drying rate decreased the probability of failure, but over the short term a rapid drying rate improved the chance of success except when the lake stage was high
- rainfall was sparse and inconsistent
  - especially if the temperature remained high
  - high rainfall increased the probability of failure if it led to an abrupt reversal of an otherwise prolonged drying trend or to a prolonged rising-water trend at high lake stages

To summarize, the probability of Tricolored Heron hatched-nest failure increased when:

- nests were initiated late in the season
- nest height and cover were low
  - the effects were only marginally significant, with cover effects more important, and a high nest may have increased the probability of failure for some pairs during incubation
- the minimum daily air temperature dropped
  - an increase in temperature increased the probability of failure following periods of rapid drying at low lake stages or if the surface-water level was rising continually
- the mean lake stage was low
  - a higher stage decreased the probability of failure over both the short and long term if combined with steadily rising water but lower rainfall (i.e., a slow rising trend), but an increase in the mean stage increased the probability of failure if it interrupted a rapid drying trend

- the lake stage was increasing rapidly or continually
  - a slower drying rate decreased the probability of failure over the short term if the temperature was high, and a slow, steady rising-water trend decreased the probability of failure at higher stages
- rainfall was high
  - high rainfall increased the probability of failure if it led to a prolonged rising water trend, particularly if it interrupted an established drying trend, but consistent long-term rainfall decreased the chance of failure

Little Blue Herons. The 30-day hydrologic variables provided the most discriminatory power among the full-cycle models, with the 14/90-day model ranking second best (AIC - 30-day = 33.0, 14/90-day = 37.4). The reverse was true for the hatching models. All models included a significant positive relationship with DJUL. The full-cycle reference model was relatively uncomplicated. High nests succeeded more often than low ones. The probability of nest failure increased during cold weather, but high temperatures increased the probability of failure during periods of rapid drying and low rainfall. A rapid drying rate decreased the probability of failure, but less so if temperatures remained high. Relatively high rainfall decreased the probability of failure unless combined with below average temperatures. No stage or DRIS effects were significant in the 30-day reference model. The only noteworthy variation evident in the suboptimal full-cycle models was that the 14 and 14/90-day models suggested that a high mean stage typically increased the probability of failure over the short term. Similarly, the hatching reference model indicated that a high short-term stage increased the probability of failure, especially if the surface-water level was rising steadily, but that a high long-term stage decreased the probability of failure. These relationships appeared to reflect the same trend evident in the Great Blue Heron full-cycle model;

i.e., that high winter surface-water levels decreased the probability of failure as long as the surface-water level dropped during the nesting season (as happened in 1989). The hatching model results for rainfall variables emphasized that high short-term rainfall increased the probability of failure if it caused a rapid reversal in a prolonged drying trend, but otherwise consistent long-term rainfall decreased the probability of failure. The 30-day hatching model also provided some evidence that a slow, steady rising-water trend at high lake stages at least did not increase the probability of failure. Finally, the hatching models differed from the full-cycle models in that no significant nest height effects were shown.

The post-hoc classification efficiency of the Little Blue Heron full-cycle reference model (93% correct overall, 94% sensitivity) was only slightly lower than for Great Egrets and Great Blue Herons, and the sensitivity rating was much higher than for the Tricolored Heron nestling model (Table 5-4). The Hosmer-Lemeshow goodness-of-fit statistic also indicated a very good fit (P = 0.988). Only one outlier observation was evident ($\Delta\chi^2$ = 16.7); the nest was unusual because it was one of the latest successes. The hatching reference model again failed to achieve the same level of efficiency as the best full-cycle model. The post-hoc classification efficiencies were lower (87% overall, 77% sensitivity), and the Hosmer-Lemeshow test statistic also indicated a greater--but still far from significant--deviation from an optimal fit ($\hat{C}$ = 2.174, df = 5, P = 0.818). In this case, two nest failures were significant outliers ($\Delta\chi^2$ = 12.5 and 26.7); both may have been cases of infertile eggs.

To summarize, the probability of Little Blue Heron nest failure increased when:

- nests were initiated late in the season
- nest height was low

  - the effect was evident only in full-cycle models, implying that the effect applied only to nests with nestlings
- the minimum daily air temperature dropped
  - high temperatures increased the chance of failure when the lake stage was low and/or following prolonged drying with low rainfall
- the mean lake stage was high (stage effects were significant but relatively unimportant compared to other effects)
  - a high short-term stage--i.e., during the nesting season--increased the probability of failure most if combined with rapidly and continually rising surface-water levels, but a high winter lake stage decreased the probability of failure
- the lake stage was not decreasing steadily
  - the benefits of rapid drying declined as the temperature increased
  - a prolonged, rapid rising-water trend increased the probability of failure most at high lake stages, but a slow, steady rising trend did not
- during cold, rainy weather
  - high short-term rainfall that led to an abrupt or prolonged reversal in an otherwise consistent drying trend also increased the probability of failure, but otherwise consistent long-term rainfall improved the chance of success

White Ibises. Both the hatching and full-cycle reference models incorporated 14/90-day mixes of hydrologic variables (e.g., Table 5-4), and in both cases the 60-day variables resulted in the second best models (full cycle 14/90-day AIC = 47.9, 60-day =

57.6). The best hatching model was far more complex (11 main effects, 11 interactions) than the best full-cycle model (6 main effects, 4 interactions; Table 5-4), suggesting that the patterns of response were less consistent during incubation.

All the full-cycle models and most hatching models indicated that a high nest reduced the chance of failure significantly (e.g., Table 5-4). Nest cover effects were much less prevalent (NCOV range 0-100, mean 39%); among the interaction models, only the hatching reference model showed a significant effect, with high cover decreasing the probability of failure ($P = 0.026$). Two of the non-interaction full-cycle models showed marginal cover effects, but indicated the opposite relationship with failure.

All of the final models again showed that the probability of nest failure increased during cold weather, with the common qualification that high temperatures increased the probability of failure during peak drought periods--i.e., at low lake stages following prolonged, rapid drying. The full-cycle reference model demonstrated that an increase in the mean short-term stage increased the probability of failure unless the temperature remained above average (Table 5-4). Over the long term, a high mean stage decreased the probability of failure if the surface-water level was rising slowly (positive DRAT90, lower RAIN90), but a lower mean stage improved the chance of success if the surface-water level was dropping rapidly. The results for DRAT90 indicated that the probability of failure declined in conjunction with a steady and rapid drying trend, but also confirmed that a slow rising trend decreased the probability of failure at high lake stages. The coefficients for RAIN90 confirmed that consistent rainfall increased the probability of nest success at low lake stages following prolonged drying, but that high rainfall increased the probability of failure at high lake stages if it contributed to a rapid rising water trend.

The complexity of the hydrologic relationships shown in the hatching reference model was bewildering. Two primary themes emerged: 1) a greater variety of relationships appeared to emphasize that low and receding surface-water levels began to increase the probability of failure once the drought reached peak intensity; 2) the probability of failure did not increase in response to rising water if the rise was slow and steady and did not constitute an abrupt reversal of an established drying trend. Referring back to the non-interaction models further suggested that a higher mean lake stage and higher rainfall decreased the probability of failure as long as the surface-water level was not rising rapidly and/or continually, and also that over the long term a slower drying rate was better, but an accelerated rate during the nesting season improved the chances for successful nesting.

The full-cycle reference model achieved a high degree of post-hoc classification efficiency (94% correct overall and 94% sensitivity), and the Hosmer-Lemeshow test confirmed a very good fit (P = 0.981; Table 5-4). Residual plots revealed three nests--two successes, one failure--that were moderate outliers ($\Delta\chi^2$ = 8.4-11.4) and two others--one success, one failure--that were borderline outliers ($\Delta\chi^2$ = 3.6 and 4.4). All three of the moderate outlier nests were initiated later than most nests in the colonies involved, and did not conform to the dominant trend shown for nest height. Again, however, I did not feel that deleting these nests was warranted. One of the borderline outlier nests was unusual in that it failed just before the nestlings reached the 14 day threshold. Two dead nestlings confirmed the failure, and it is possible that disease was involved. The other was one of the earliest successes and again did not conform to the dominant trend for nest height. As was true for other species, the hatching reference model did not achieve the same level of post-hoc classification efficiency as the best full-cycle model (83% correct overall, 89% sensitivity), and the Hosmer-Lemeshow test

confirmed a poorer, but still good fit ($\hat{C}$ = 5.417, df = 5, P = 0.413). Residual plots identified three failures and one success that were moderately strong outliers ($\Delta\chi^2$ = 13.7-18.6). Two of the nests were unusual because they failed just before or perhaps just after hatching, possibly due to predation. There was no obvious reason why the other should be an outlier. The successful nest was unusual because it was initiated late in the season, and in fact the single surviving nestling probably died at around 17 days.

To summarize, the probability of White Ibis nest failure increased when:

- nests were initiated late in the season
- nest height was low
- the minimum daily air temperature dropped
  - high temperatures increased the probability of failure at very low lake stages following prolonged drying
- the mean lake stage was high and the surface-water level either rose or dropped abruptly and rapidly
  - the combination of a high mean stage and slowly but steadily rising or falling surface-water levels decreased the probability of failure, but at lower stages rapid drying improved the chance of success
- rainfall was sparse and inconsistent
  - high rainfall decreased the probability of failure if it maintained a steady rising trend, but not if it caused an abrupt, rapid increase in surface-water levels or if the rising trend was prolonged
  - an increase in rainfall decreased the probability of failure at the height of the drought--i.e., at low lake stages following prolonged drying;

otherwise, a rainfall driven reversal of an established drying trend increased the probability of failure

Discussion

Model-Building Strategy

Generally high post-hoc classification efficiencies and low Hosmer-Lemeshow test statistics, consistently high likelihood ratio χ^2 for covariates statistics, and few outlier observations demonstrated that all models except the combined Snowy Egret/Tricolored Heron hatching model performed very well for identifying the determinants of nest failure. Proceeding through the process of analyzing the full range of models, with and without interaction terms and with the different sets of hydrologic variables, proved to be a valuable approach. Ignoring the interaction terms would have precluded the exposure of subtle influences, such as high temperatures becoming detrimental during peak drought periods. Conversely, referring to the non-interaction models helped identify consistencies and confirm principal relationships.

The final logistic regression models presented by Frederick and Collopy (1989a) and Frederick and Loftus (1993) were less complex than those presented herein, despite each team having considered similar independent variables and having gathered data in roughly similar Everglades-type marsh ecosystems. One primary difference is that I considered interaction terms in my models and many turned out to be highly significant, but a greater variety of main-effects variables were significant in my models, as well. In my experience, the backward-selection approach to model building resulted in more robust--and usually more complex--models that better summarized the variation in the datasets than models selected by the automated

stepwise-selection routine available through the SAS LOGISTIC module. Besides having employed the stepwise selection method, the previous authors also assigned an initial significance level of 0.05 as the selection criteria to guide the automated procedure. The combination may have resulted in unnecessarily conservative final models (Hosmer and Lemeshow 1989: 87-88; Burnham and Anderson 1992).

I believe the backward selection method produced more realistic models because the climatic and hydrologic variables usually were correlated, often to a high degree. Beginning with a full model accounted for important confounding effects that a stepwise or forward selection routine might never have allowed to emerge (Hosmer and Lemeshow 1989: 86). One of a pair of correlated variables should be eliminated only if careful consideration reveals that the information contained in the variables is truly redundant. In my study, the DRAT and DRIS variables within a given time-horizon always were highly and positively correlated (Pearson $r > 0.90$). Nonetheless, my experience suggested that including both variables frequently accounted for significant and unique influences of two aspects of changing surface-water levels: the magnitude and regularity of change. Because I employed both AIC and other goodness-of-fit statistics to guide the selection of variables and models, I believe my final models represented a good balance between parsimony and precision (Burnham and Anderson 1992). In all instances where I retained both the DRIS and DRAT variables, the improvement in the AIC score was substantial.

Different approaches to model building probably contributed to the difference in complexity alluded to above; however, another primary and perhaps more important reason for the difference is that the two studies were conducted in different subregions of Florida and in different years (1986-87 versus 1989-91). The range of climatic and

hydrologic influences that affected nesting birds during each study differed in important ways (see below).

Date of Nest Initiation Effects

My analyses confirmed for all species that, with several other significant environmental factors accounted for, the later the date of initiation the greater the chance of failure. A variety of proximate environmental factors could reduce the productivity of late nests. Kushlan et al. (1975) surmised that early-nesting Wood Storks in the Everglades achieved higher success because they were able to fledge young before the onset of heavy summer rains and large-scale reversals in drying trends. Frederick and Collopy (1989a) studied environmental determinants of White Ibis nest failure in the Everglades using logistic regression, and applied the same reasoning to explain a positive relationship between failure and initiation date. A similar analysis of data for Great Egrets from the Everglades revealed the same positive relationship, but the authors provided no explanation for the trend (Frederick and Loftus 1993: Table 1. Comments in the text misrepresent the results; P. C. Frederick pers. comm.). Factors such as the onset of heavy summer rains undoubtedly reduce survival toward the end of the season, but including temperature, hydrology, and nest situation variables in the multiple-regression models should have largely accounted for consistent seasonal trends in rainfall and other environmental influences. It is possible that the DJUL variable integrated a variety of hydrologic and climatic influences that independently might not have accounted for prominent seasonal trends in nest failure. However, another possibility is that the consistent positive relationship between date-of-initiation and the probability of nest failure reflected the influence of breeder competence. The trend is consistent with the hypothesis that, among species with a

restricted breeding season, nest success and productivity should decline through the season because the most experienced and competent breeders tend to be the first to nest (e.g., Lack 1966; Johnsgard 1973; Newton 1979: 106; Skutch 1976: 278-279; Rodgers 1978; Ryder 1980; Pratt and Winkler 1985).

Nest Height and Cover Effects

Nest height influenced to some degree the nest success of all species except Great Egrets. High Great Blue Heron nests failed more often because the tops of taller willow trees were the most likely to break or to oscillate enough to displace eggs or nestlings under the strain of high winds (10 of 76 or 13% of all failures; Chapter 4). A high nest also apparently increased the probability of failure for some Snowy Egrets and Tricolored Herons with eggs. My field observations suggested that high and exposed nests were more susceptible to predatory Fish Crows and Boat-tailed Grackles. I rarely could confirm a true predation event or attribute the loss of a whole nest to egg predation; however, crows and grackles were usually present at all colonies, scavenged abandoned eggs, and at least attempted to take advantage when the presence of researchers temporarily disturbed the adult wading from their nests (Chapter 4). Crows are common predators at wading bird colonies (Shields and Parnell 1986; Bancroft et al. 1990; Bildstein et al. 1990; Frederick and Spalding 1994), and Jenni (1969) previously implicated grackles as egg predators. Losses to such aerial predators may occur only when nesting adults are already stressed and less attentive at their nest, or when the presence of a researcher disturbs adults from their nests (Frederick and Spalding 1994).

The opposite nest-height trend was shown for Snowy Egrets, Tricolored Herons, and Little Blue Herons with nestlings, and for White Ibises--particularly in the full-cycle

models. Burger (1978) provided evidence that most species of wading birds tend to seek the highest nests if not hindered by competition from larger or more aggressive species, or already settled conspecifics. Nests situated near the top of the vegetation canopy are probably easier for adults to land on, and such placement may facilitate vigilance against aerial predators, as well as restrict access by ground or aquatic predators such as alligators. However, another explanation may have applied to White Ibises with nestlings. Field observations suggested that ibis nestlings in low nests were particularly prone to jump and run rather than try to climb into the canopy when disturbed by a researcher. This might have resulted in higher nest failure among low nests if the dispersed nestlings failed to relocate their nests or perished by drowning in muck under the colony (Chapter 4). It was important to note that the NHGTxNCOV interaction term was also significant in the White Ibis hatching reference model, and indicated that a high nest decreased the probability of failure during incubation, but more so if nest cover was also high. This detail may indicate that exposed White Ibis eggs were also more subject to attack by crows and grackles. The only other case in which nest-cover effects approached significance was in the Tricolored Heron nestling model, wherein the relationship with failure was negative. This trend, although relatively weak, may reflect the influence of Black-crowned Night Herons, which are well-known predators of small nestlings (Frederick and Collopy 1989b) and nested interspersed with other species in several colonies. Strong circumstantial evidence suggested that several broods of very young Snowy Egret and Tricolored Heron nestlings were taken by the same adult night-herons whose nestlings at one point regurgitated several young Cattle Egret chicks. The white species may have been easier targets to locate; perhaps an increase in exposure was necessary to render the more cryptic Tricolored Heron nestlings susceptible.

Temperature Effects

Cold temperatures have been implicated in delays of nesting cycle initiation among Wood Storks (Kahl 1964), Great Egrets (Simmons 1959), and White Ibises (Rudegeair 1975), and in the general reduction of nesting attempts among several species (Ogden et al. 1980). My analyses demonstrated that cold temperatures resulted in a significantly higher probability of nest failure for all species. Frederick and Loftus (1993) confirmed the same relationship for Great Egrets in the Everglades. Cold temperatures could conceivably directly affect the health of eggs and young, but Simmons (1959) found that incubating Great Egrets were not adversely affected by cold temperatures and snow in Louisiana, and all the study species range into much more temperate regions than southern Florida (Palmer 1962). Moreover, Frederick and Loftus (1993) demonstrated that cold temperatures significantly reduce the activity levels of small fishes and increase their tendency to flee and to burrow and hide. Therefore, the negative relationships between the probability of nest failure and ambient temperature, and delays in colony initiation due to cold temperatures, are most likely responses to reductions in the accessibility of prey (Frederick and Spalding 1994).

Significant interaction terms in my models frequently revealed limits to the benefit of higher temperatures. In particular, high temperatures became a liability at the height of the drought in shallow habitats if rainfall remained scarce. On several occasions during the 1990 drought season, I recorded surface-water temperatures as high as 43-45°C in shallow water. Such high temperatures probably increased mortality or at least the rate of emigration to deeper water among potential prey organisms. If so, wading bird foraging efficiency would have declined. The Great Egret models and the Snowy Egret and Tricolored Heron nestling models also suggested that the

combination of high temperatures and rapidly or continually rising water was not favorable. If the activity levels of small fishes and other prey increase with increasing temperature (Frederick and Loftus 1993), then high temperatures may amplify the dispersal of prey (e.g., small fishes, amphibians, macroinvertebrates) responding to a rainfall-driven expansion of flooded marsh. Rapid dispersal of prey would render wading bird foraging at least temporarily less efficient, because the relative abundance of prey would decline and the distribution of small schooling fishes would become increasingly patchy.

Hydrologic Effects

All final models included one or more of the hydrologic variables, and the combined contribution to discriminatory power always was substantial. This confirmed the validity of the logical assumption that surface-water hydrology influences wading bird foraging and therefore nesting ecology. Four of the six best full-cycle/nestling models incorporated either only long-term hydrologic variables or the 14/90-day mix. The exceptions were Little Blue Herons and Snowy Egrets, for which the 30-day variables provided the most discriminatory power. The Great Egret hatching reference model also incorporated the 30-day variables, but all other hatching reference models incorporated the 14/90-day mix. Moreover, in all cases but one (the Snowy Egret nestling model) where the 14/90-day mix did not result in the best final model, it ranked second best. In contrast, the shortest term 14-day variables alone never resulted in a best final model. These results suggested that moderate to long-term hydrologic trends were most important for determining levels of nest success, but short-term changes also influenced levels of tenacity, particularly during incubation. It is possible that the short-term variables would have ranked higher in importance if I had collected

hydrologic data at a finer scale of spatial resolution; open-water lake-stage measurements undoubtedly do not adequately reflect local hydrologic variations in the littoral zone (Chapter 2). Nonetheless, it seemed appropriate that the importance of long-term variables was reflected most strongly in the full-cycle models for the two species that take the largest and slowest growing prey (Willard 1977; unpubl. data) and have the longest nesting cycles: Great Egrets and Great Blue Herons. Furthermore, if the tenacity with which birds pursue a given nesting effort increases as the investment in time and energy grows (Skutch 1976: 441), incubating birds are probably more apt to respond to recent, detrimental changes in foraging conditions by abandoning the effort. In contrast, once a nesting pair has invested to the point of hatching young, they are probably less likely to abandon due to minor or short term changes in hydrologic and therefore foraging conditions. Longer-term hydrologic variables may better reflect the overall quality of foraging conditions and therefore better predict whether nesting pairs will ultimately succeed in fledging young.

Besides the aforementioned possibilities concerning model design, the difference in model complexity evident when comparing my models and those developed by Frederick and Collopy (1989a) and Frederick and Loftus (1993) probably reflects variation in the hydrologic and climatic forces that affected the birds during the two studies. Specifically, during my study the drought created a situation where, over the long term, consistent rainfall increased the chance of nest survival for most species. Consistent but moderate rainfall probably enabled isolated, shallow wetland areas to persist and helped maintain the health of prey populations concentrated by the drought (also see Maddock and Baxter 1991), without causing large-scale reversals in established drying trends. Bildstein et al. (1990) found that high spring rainfall led to increased reproductive effort among White Ibises in South Carolina, because high

rainfall was necessary to maintain crayfish populations in the shallow, forested wetlands where the nesting adults foraged. In contrast, the Everglades were "particularly wet" during the two years studied by Frederick and Collopy (1989a). Accordingly, rainfall was not a significant determinant of nest failure for White Ibises and was a significant positive determinant of failure for Great Egrets (revised analysis in Frederick and Loftus 1993). Moreover, high rainfall was implicated as a cause of whole-colony instability (also see Bancroft and Jewell 1987; Frederick et al. 1992). The interaction terms in my models often accounted for both the positive drought and negative high-water influences of rainfall. In addition, the variety of models and different sets of hydrologic variables frequently confirmed that reversals due to high short-term rainfall increased the probability of failure.

My study confirmed that White Ibises depended on favorable hydrology to achieve high nest success, and that sustained surface-water recessions generally increased nest survival (cf. Frederick and Collopy 1989a; Frederick and Spalding 1994). However, my results suggested that the probability of nest failure among ibises did not increase if the transition to rising water was gradual, and that a rapid rate of recession improved the chances of success only at lower lake stages. Kushlan (1974) previously noted that foraging White Ibises concentrated in similar numbers at optimal depths during periods of rising as well as receding water. Regurgitant left at nests and observations of foraging birds (pers. observ. and unpubl. data) indicated that invertebrates such as insects, worms, and snails were the most common prey of ibises at the lake. The species also consumed crayfish, but not as exclusively as in many areas (e.g., Kushlan and Kushlan 1975; Bildstein et al. 1990). White Ibises captured more fish at the height of the drought (unpubl. data) when large flocks of all species collected in shallow, open flats scattered between thick beds of exposed submerged

vegetation (Chapter 2). The prolonged drying and low surface-water levels brought by the drought may have concentrated prey enough to enable the ibises to switch to fish (Kushlan 1976c, 1979; Frederick 1993). Otherwise, it appeared that ibises usually focused on invertebrate prey at the lake, and often concentrated along rising and falling water fronts and in newly flooded areas both on and adjacent to the lake (Chapter 2; pers. observ.). White Ibis nestling production in nests that succeeded in producing at least one young to the threshold age of 14 days was highest for the study in 1989 and only slightly lower in 1990 (Chapter 4). However, although ibis productivity was reduced in 1991 when no spring surface-water recession occurred, the reduction was slight, confirming that the species could also succeed during periods of fluctuating and rising surface-water levels.

During this study, all species were most productive during the 1989 and especially the 1990 drought seasons (Chapter 4), and the regression analyses confirmed that the probability of nest failure decreased most among both White Ibises and the ardied species during periods of receding water and lower lake stages. Colony histories documented through aerial surveys indicated that high and fluctuating surface-water levels in 1991 and 1992 contributed to whole-colony instability among the small ardeids (Chapter 4). The regression results, however, indicated that Snowy Egrets were more successful when the long-term drying rate was relatively slow, and did better at high stages when the short-term drying rate was slow. In addition, rapidly receding water became a detriment to nest survival for all species after the drought intensified and the lake stage reached record low levels. Furthermore, the combination of a slow, steady rising-water trend and higher lake stages did not increase and may have decreased the probability of failure for several species (particularly for Great Egrets and White Ibises, but probably not for Snowy Egrets). As alluded to in the discussion of

temperature effects, an abrupt reversal of a prolonged drying trend most likely would reduce wading bird foraging efficiency, at least temporarily. Large-scale reversals in normal spring drying trends have caused widespread abandonment in the Everglades (Kushlan 1987; Frederick and Collopy 1989a; Bancroft et al. 1994; Frederick and Spalding 1994). However, if a reversal is not severe enough to cause immediate abandonment, most species may eventually be able to profit by switching their attention to the flooding front or to reflooded off-lake pocket wetlands where the drowning and exposure of terrestrial organisms and the hatching of ephemeral aquatic invertebrates, fishes, and amphibians may enable profitable foraging.

It was less clear why Snowy Egrets might not have capitalized on flooding-front concentrations. The species was strongly inclined to forage--often using aerial techniques--from floating mats of water hyacinth and from the large surface leaves of lotus scattered through deeper, prey-rich Hydrilla beds (Chapter 2). Such habitat mixes proliferated in late 1990 and in 1991 following the drought. The reproductive effort, nest success, and productivity of Snowy Egrets in 1991 was only slightly lower than in 1990, and was comparatively higher in 1991 than for most species (Chapter 4). A stronger reliance on floating-mat, deep-water habitats for foraging during periods of rising water when shallow-water concentrations of prey were unavailable (e.g., during 1991; Fig. 5-2) might have precluded the development of a negative relationship between failure and gradually rising water. Tricolored Herons readily used the mixed lotus and Hydrilla habitats as well (Chapter 2), and achieved higher success in 1991 than most species (Chapter 4), but also apparently profited from slowly rising water when the lake stage remained high (i.e., most likely in 1991; Fig. 5-2).

Great Blue Herons and Great Egrets initiated the most nests in years that began with high lake stages (i.e., in 1989 [Fig. 5-2] and in 1992); however, the nest success

and per nest productivity of both species was highest during 1990 when the scenario included only moderate winter lake stages and a protracted spring recession (Chapter 4). The regression models confirmed the benefits of a relatively low lake stage and receding water, but a secondary trend in the Great Blue Heron model suggested that high winter water stages decreased the probability of failure as long as a spring recession brought the stage down during the nesting season (i.e., the conditions in 1989; also see Frederick and Spalding 1994; Loftus and Eklund 1994; Ogden 1994). Little Blue Herons also initiated more nests in 1989 than other years, but unlike for the former species, the same was not true in 1992. This suggested that, although the larger species may frequently respond favorably to high winter surface-water levels, Little Blue Herons apparently responded to another cue.

Loftus et al. (1990) provided evidence that long-hydroperiod marshes in the Everglades generally support higher densities of small fishes and macroinvertebrates than short-hydroperiod marshes. Loftus and Eklund (1994) provided additional evidence that densities of both large and small fish--and presumably many macroinvertebrates--increased during prolonged periods without a large-scale surface-water recession. Thus, a large-scale recession following a long period of high water should result in unusually dense concentrations of many prey species, and would thereby generally enhance wading bird foraging conditions. One of the most dramatic hydroperiod effects documented in Loftus et al. (1990) involved grass shrimp. Grass shrimp constituted 47% of the aggregate mass of prey fed to Little Blue Heron nestlings at Lake Okeechobee in 1989 (McIvor and Smith 1992). Frederick and Collopy (1988) also found that grass shrimp were an important prey species for Little Blue Herons in the Everglades. Throw-trap sampling conducted during the study showed that grass shrimp decreased in abundance relative to small fishes in shallow areas (i.e., water

depth <20 cm), but otherwise occurred in a variety of vegetation types (McIvor and Smith 1992). These data suggest that grass shrimp are more likely than forage fish to migrate or perish when surface-water levels drop. Little Blue Herons, therefore, may have encountered the best foraging conditions in 1989, after the lake stage had dropped considerably and prey became concentrated, but before the drought resulted in very low lake stages and their favored prey were eliminated from a wide range of previously occupied upper-elevation habitats. Conversely, the other ardeid species all specialize to a greater degree on fishes (Frederick and Collopy 1988; Frederick and Spalding 1994), and may not have gained maximum advantage until the lake stage dropped to even lower levels in 1990 (Fig. 5-2) and fish and other prey were heavily concentrated in and between exposed beds of submerged vegetation (McIvor and Smith 1992; Chick and McIvor 1994).

Conclusion

Dramatic drought-related declines in the lake stage enhanced some aspect of all species' nest success and productivity, but species-specific responses differed in subtle ways and the regression models often indicated a high degree of complexity with regard to the environmental determinants of nest failure. The full-cycle and nestling reference models all achieved a high degree of discriminatory efficiency, despite having incorporated spatially coarse-scale hydrologic data. I speculate that if I had collected both temporally and spatially fine-scale data, the regression models would have indicated even greater complexity. The relative simplicity of the non-interaction models was attractive, and the general trends indicated in these models usually were also reflected in the more complex interaction models. However, it was clear that including the interaction terms revealed a variety of important exceptions to the general trends. It

was fortunate that my study coincided with an unusual natural event that forced the birds to respond to an unusually wide range of environmental conditions. As a consequence, my analyses revealed more complexity than would have arisen if conditions had varied less.

I did not herein explicitly consider the influence of disease on nestling survival (Frederick and Spalding 1994). Spalding et al. (1994) showed that parasitic infections of the nematode Eustrongylides ignotus increased nestling mortality and reduced nestling growth rates among Great Egrets at the lake in 1990; however, disease rarely could be unequivocally assigned as the cause of whole-nest failure (Chapter 4). Hydrologic trends may influence the distribution and abundance of Eustrongylides in some way (e.g., complete drying of sites), but most evidence suggests that substrate-type, disturbance levels, and nutrient-input histories are probably the primary determinants of the species' distribution (Spalding et al. 1993). I also did not focus on the results of aerial following-flight studies, which showed that all species consistently depended to some degree on off-lake foraging habitats (McIvor and Smith 1992; unpubl. data). The latter may yield a level of independence from on-lake hydrology; for instance, nesting Great Egrets routinely panhandled fish scraps at cleaning stations and stole minnows from bait houses to feed their young (McIvor and Smith 1992; unpubl. data). Despite the possibility that these other factors may represent additional and important complexities, the model-building exercise illuminated a variety of relationships that conformed to expectations based on field observations, analyses of related data, and previous studies.

My analyses confirmed that nesting wading birds generally benefit from spring surface-water recessions, and that at the lake a lower stage that exposes a wide variety of marsh habitat to foraging birds also generally increases the probability of nest

success. However, it appeared that nest failure rates began to increase among most species once the drought reached its peak and the lake stage was very low, temperatures remained high, and rainfall was scarce. The same drought brought disaster for many colonies of wading birds in the Everglades, because most marsh areas dried completely; only the downstream, deep-pool areas of the diked Water Conservation Areas remained wet and served as refuges for displaced wading birds (Bancroft et al. 1994; Hoffman et al. 1994). The lake was also far from dry at the height of the drought, and served as an important refuge for foraging wading birds, especially in 1990 (Chapter 2). However, the variation in reproductive effort and productivity among the species studied was not as pronounced as variation in the size of the larger foraging population might have suggested. Moreover, the two largest 1990 nesting colonies (Clewiston Spit and Eagle Bay Island; Fig. 5-2) were not situated near the area where most foraging activity ultimately was concentrated (i.e., in Fisheating Bay; see Chapter 4 and compare Bancroft et al. 1994). Thus, although the per nest productivity of most species was highest in 1990, late nesting pairs may have experienced stress when the drought reached maximum intensity in June. Moreover, the lake did not attract large numbers of foraging birds in 1991 when the lake stage remained moderate and relatively stable, but most species were apparently able to continue nesting successfully if the surface-water level was rising slowly and the transition to rising water was not too abrupt. Thus, management strategies applied to the lake should explicitly recognize the following:

1) Patterns of fluctuation in the abundance and habitat use of foraging and nesting populations may not always coincide.

2) Although a protracted spring surface-water recession to at least moderate lake stages is probably the ideal, most species may be able to nest successfully at the lake

under a variety of hydrologic scenarios, particularly if a diverse array of alternative foraging habitat is available adjacent to the lake.

3) Given #2 and evidence that periods of high water foster more abundant and widespread prey (Loftus and Eklund 1994), but periods of low water and associated disturbances such as fire foster diverse and healthy plant communities (David 1994a; Gunderson 1994; Richardson and Harris 1994), management plans should be flexible enough to accommodate natural hydrologic variability so as to insure a resilient system.

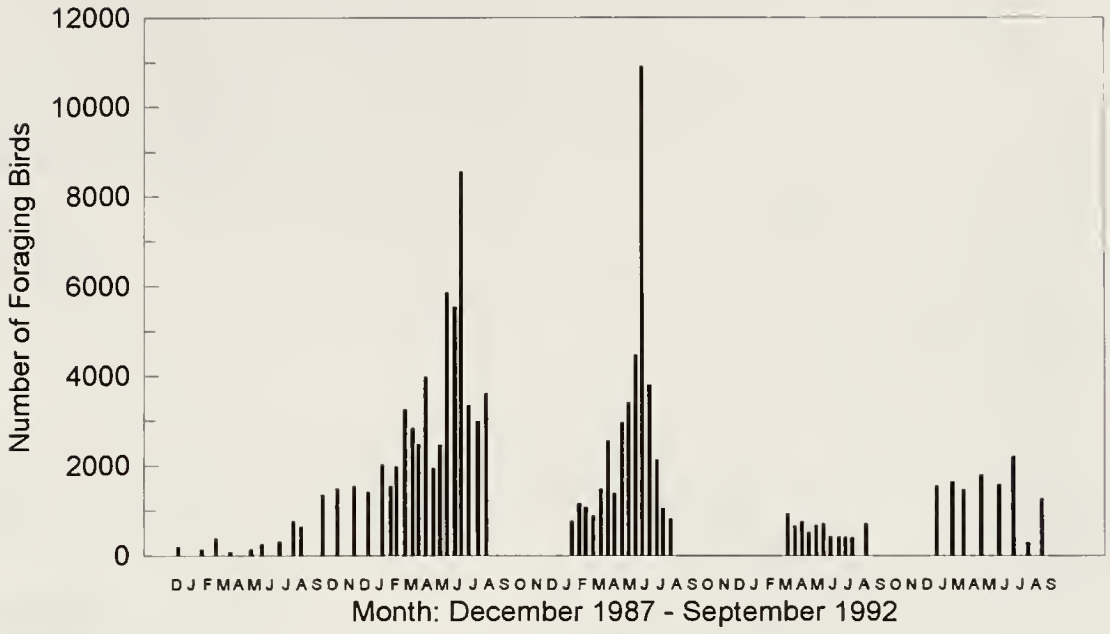
CHAPTER 6
AN ENERGY-CIRCUIT POPULATION MODEL FOR GREAT EGRETS

Introduction

Population studies of wading birds conducted from 1988-1992 revealed that fluctuating surface-water levels are the primary determinant of foraging and breeding population numbers and diversity, and of breeding effort and success at Lake Okeechobee, Florida (Chapters 2, 4, 5). Systematic aerial surveys demonstrated that the foraging populations of six primary species increased substantially during periods of steady and sustained surface-water recession at lake stages below approximately 4.3 m NGVD (Chapter 2; NGVD = National Geodetic Vertical Datum of 1929, essentially equivalent to height above mean sea level; for convenience, I will henceforth omit the NGVD qualifier). The highest numbers of all species--including large numbers of uncommon Wood Storks and Roseate Spoonbills--were observed during peak drought periods in 1989 and especially 1990 when the lake stage dropped to a 10-year low of 3.2 m. Foraging activity at these times was constrained to limited areas of outer littoral zone habitat featuring exposed submerged vegetation. Prey sampling confirmed that these habitats harbored unusually high concentrations of small fishes and other prey organisms (McIvor and Smith 1992; Chick and McIvor 1994); however, most of the Everglades and other palustrine habitats in the region were dry, and otherwise deep-water lacustrine and pooled habitats served as regional refuges for wading birds at this time (Chapter 2; Hoffman et al. 1994). Concurrent nesting studies indicated that the

number and diversity of suitable colony sites declined during the 1990 peak drought year, with most activity restricted to island sites (mostly dredge-spoil piles) still surrounded by water (Chapter 4). Great Blue Herons and Great Egrets--the two largest species--initiated the most nests in 1989 and 1992 when the season began with a relatively high lake stage, and Little Blue Herons were unusual because they initiated twice as many nests in 1989 as in 1990, and fewer in 1991 and 1992. Otherwise, despite the smaller number of colonies, the other three species initiated the most nests in 1990, and all species achieved the highest nest success and productivity during the 1989 and especially 1990 drought years. In contrast, the 1991 season featured comparatively stable (no protracted spring recession) and moderate lake stages, and most species responded with lower reproductive effort (i.e., fewer nests) and success. The lake stage returned to and remained at high levels in 1992. A moderate-paced late-winter/spring recession occurred and elicited at least moderate reproductive effort among all species except Little Blue Herons; however, the recession was unsteady and interrupted prematurely by early summer rainfall. This weather pattern contributed to several colony abandonments among the smaller ardeid species and resulted in low to moderate nest success among all but Great Blue Herons. A comprehensive logistic regression analysis confirmed that the probability of nest failure was lowest at low to moderate lake stages during steady surface-water recessions (Chapter 5). Along with hydrologic trends, date of nest initiation and minimum daily air temperature were also significant determinants of nest survival for all species. Cold temperatures reduced survival rates among all species and contributed to large-scale nest abandonment among early-nesting Great Blue Herons and Great Egrets in 1989 and 1991; however, with temperature effects accounted for, the probability of failure always increased as the season progressed.

To conceptually integrate the above findings and further examine the validity of the conclusions for one common species, I programmed an energy circuit model to simulate the annual population cycles of Great Egrets (Odum 1971, 1983). From August 1988 through August 1992 (no surveys September through December 1989-1992), the estimated number of Great Egrets foraging within the diked confines of the lake varied from a low of 281 birds in August 1992 to a high of 10,918 birds in June 1990 (Fig. 6-1a; see Chapter 2 for survey methods). The estimated peak number of active nests varied from a low of 265 in 1990 to a high of 982 in 1989 (Fig. 6-1b). The proportion of successful nests (those that succeeded in producing at least one 21-day old nestling) varied from a low of 7% in 1989 to a high of 53% in 1990, and nestling production in successful nests ranged from a low of 1.3 21-day nestlings per nest in 1992 to a high of 2.3 per nest in 1990 (Fig. 6-2 and see Chapter 4). Variation in foraging and nesting population counts therefore did not follow the same trends, and peaks in reproductive effort did not match those for nest success and productivity. With these facts in mind, my objectives in conducting this modeling exercise were threefold: 1) I sought to develop a biologically plausible mathematical model that reproduced the observed trends in abundance of the foraging and nesting populations, and in the nest success and productivity of one common species; 2) I sought to gain additional insight into the mechanisms by which different climatic and hydrologic forces interacted to influence the ecology of foraging and nesting populations at the lake; 3) I sought to determine whether modeling the apparent environmental and energetic relationships involved would help confirm that nesting birds responded to different cues than the general foraging population.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6000
4000
2000
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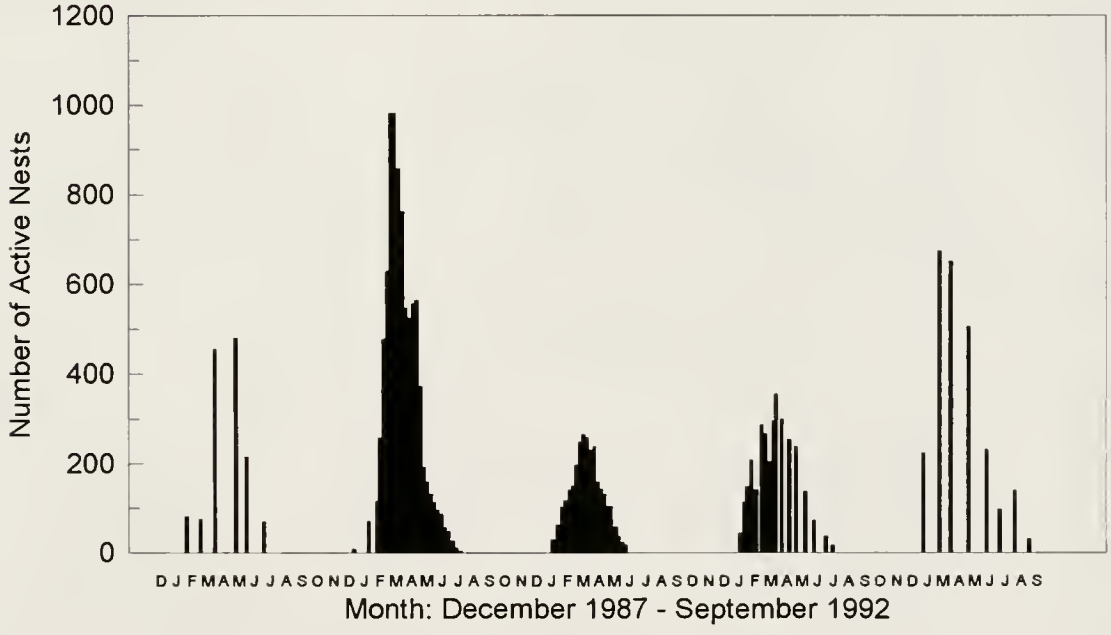
Month: December 1987 - September 1992

(a)


1200
1000
800
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200
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Number of Active Nests
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Month: December 1987 - September 1992

(b)

Figure 6-1. Estimated numbers of a) foraging Great Egrets and b) active Great Egret nests on Lake Okeechobee from December 1987 through August 1992. Extended gaps in foraging-bird counts indicate no surveys. Data for December 1987 through July 1988 were provided by the South Florida Water Management District (see David 1994a, b).

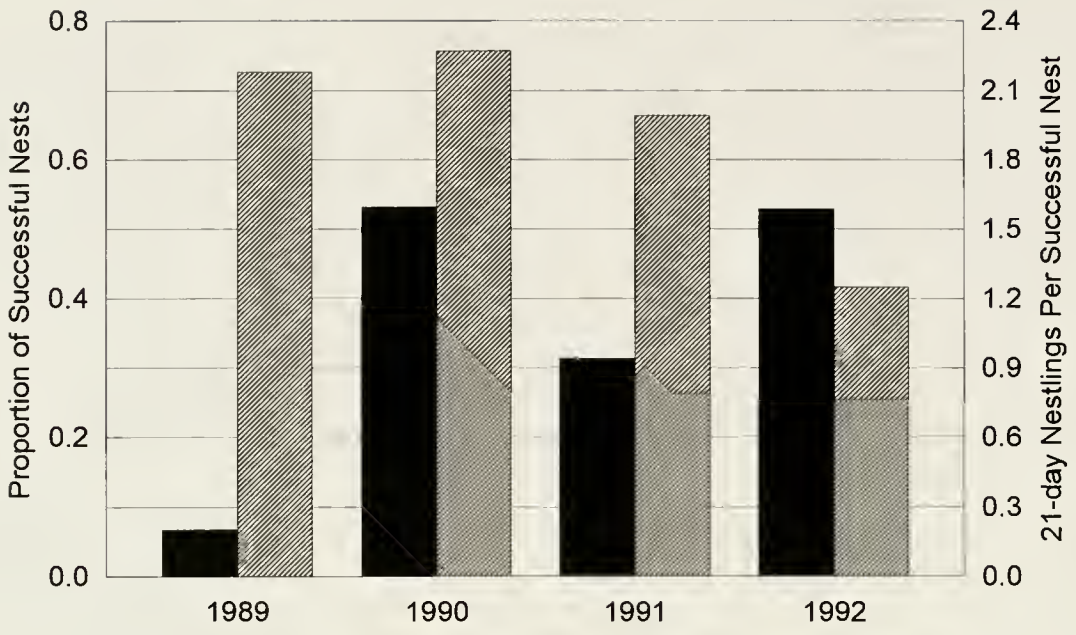


Figure 6-2. Estimates of lakewide nest success (solid bars) and nestling production (hatched bars) for Great Egrets from 1989-1992. Nest success equals the proportion of nests that succeeded in producing at least one 21-day old nestling: Mayfield estimates for 1989-1991; standard percent-survived estimate for 1992 (see Chapter 4 for details).

Study Area

Lake Okeechobee is a large (1,732 km^2), shallow (mean water depth 2.7 m), and highly regulated subtropical ecosystem. It drains a 12,000 km^2 watershed from the northwest through primarily the Kissimmee River, and is the primary source of water for the Everglades. The lake ecosystem includes a large expanse of emergent marsh (400 km^2 on average) along the western and southern margins that supports wading bird foraging and nesting activity. The lake is surrounded almost entirely by a reinforced earthen dike and water flows are controlled by a series of perimeter locks, hurricane gates, and pumping stations. The South Florida Water Management District (SFWMD), the US Army Corps of Engineers, and the State of Florida Department of Environmental Regulation oversee management of the lake under a multiple-use mandate that attempts to fill needs for flood control, human and agricultural water storage and supply, a multi-million dollar commercial and sport fishing industry, and a variety of recreational and other wildlife-related interests. Management of lake water levels is therefore a primary and often controversial concern, and the comprehensive Lake Okeechobee Ecosystem Study--of which my research was a part--was initiated in 1988 (funded by the SFWMD) to establish a baseline ecological dataset to guide the development of an ecologically-sound management strategy. Aumen (1994) provides a more detailed overview of the physiography and hydrology of the lake and its management history.

Model Formulation and Quantification

The energy-circuit diagram of the population model in its final form is displayed in Figure 6-3. Odum (1971, 1983) discusses the evolution of and principles behind the

Figure 6-3. Energy circuit diagram of Great Egret population model.

DEFINITIONS:

Forcing functions: SUN = solar input, MON = month, WA = surface water area, MINT = daily minimum air temperature, STG = daily lake stage, DR = 30-day surface water drying rate

Other variables: DENS = prey biomass density, AFR = average adult food requirement, PFA = relative prey flow to adult Great Egrets, NBRNEW = number of new breeders, CL = mean clutch size, NENEW = number of new eggs

Switches: HATSW = hatching lag switch, FLGSW = fledging lag switch, MATSW = annual maturation switch

Storages: BP = biomass of prey, NB = number of adult Great Egrets, BIOM = biomass of adult Great Egrets and food, NBR = number of breeding Great Egrets, NE = number of eggs, NN = number of nestlings, NF1 = number of fledglings aged <1 year, NF2 = number of subadults aged 1-2 years, NF3 = number of subadults aged 2-3 years

FLOW DESCRIPTIONS:

JR = useabe solar energy, J1 = gross prey production, J2 = density-dependent prey mortality, J3 = prey respiration, J4 = prey mortality not due to wading birds, J5 = Great Egret prey consumption, J6 = non-Great Egret wading bird prey consumption, J7 = adult Great Egret mortality, J8 = recruitment of breeding Great Egrets, J9 = egg laying, J10 = egg losses, J11 = egg hatching, J12 = nestling mortality, J13 = fledging, J14 = fledgling/first-year-subadult mortality, J15 = maturation of first-year subadults, J16 = second-year subadult mortality, J17 = maturation of second-year subadults to third-year subadults, J18 = maturation of second-year subadults to adults, J19 = third-year subadult mortality, J20 = maturation of third-year subadults, J21 = emigration, J22 = immigration

EQUATIONS REPRESENTED BY NUMBERED BOXES:

(1) = 1 - EXP(-4 * WA) (2) = [LOG(BP / WA)] * [1 / (1 + 600 * EXP(-0.55 * MINT))] * [(0.03 - DR) * 33.333]

(3) = [((1 + COS((MON - 3) / 0.75)) / 2) * C1] * [1 / (1 + 10^5 * EXP(-3 * STG))], with C1 = 0 if MON is 15 May - 15 December, 1 otherwise

(4) = [0.5 / (1 + 1E-5 * DENS^4)] + [1 / (1 + 5 * EXP(-500 * DR))]

(5) = (1 / (1 + 10^4 * DENS^-2.8)) * ((0.03 - DR) * 33.333) * (0.35 + 3.25 * EXP(-5 * (STG -3))) * (1 + 5.4E-4 * NB * EXP(-5E-4 * NB)

EQUATIONS OF STATE:

$$DBP / DT = [K1 * [SUN / (1 + K0 * BP * (1))]^{= J_R} * BP * (1)]^{= J_1} - [K2 * BP * BP]^{= J_2} - [K3 * BP * BP / WA]^{= J_3} - [K4 * BP / WA]^{= J_4} - [K5 * (NB + NN + NENEW) * (2)]^{= J_5} - [B6 * J5]^{= J_6}$$

$$DNB / DT = - [K7 * NB]^{= J_7} + [K18 * NF2]^{= J_{18}} + [K20 * NF3]^{= J_{20}} - [K21 * NB * (4)]^{= J_{21}} + [K22 * (5)]^{= J_{22}}$$

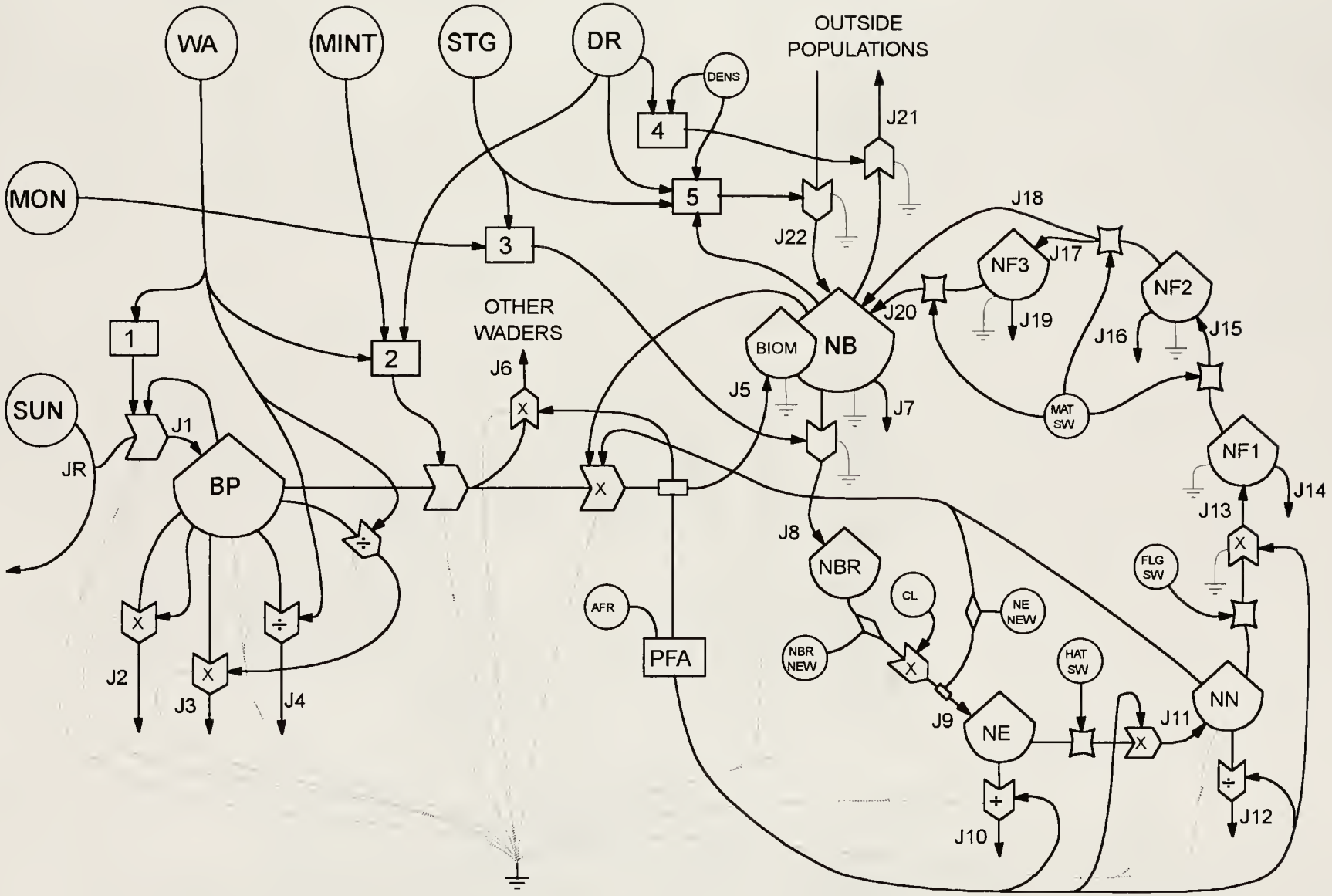
$$DNBR / DT = [K8 * NB * (3)]^{= J_8} / DT \qquad DNE / DT = [K9 * NBRNEW * CL]^{= J_9} / DT - [K10 * NE / PFA]^{= J_{10}} - [K11 * NE * HATSW * PFA]^{= J_{11}}$$

$$DNN / DT = [K11 * NE * HATSW * PFA]^{= J_{11}} - [K12 * NN / PFA]^{= J_{12}} - [K13 * NN * FLGSW * PFA]^{= J_3}$$

$$DNF1 / DT = [K13 * NN * FLGSW * PFA]^{= J_{13}} - [K14 * NF1]^{= J_{14}} - [K15 * NF1 * MATSW]^{= J_{15}}$$

$$DNF2 / DT = [K15 * NF1 * MATSW]^{= J_{15}} - [K16 * NF2]^{= J_{16}} - [K17 * NF2 * MATSW]^{= J_{17}} - [K18 * NF2 * MATSW]^{= J_{18}}$$

$$DNF3 / DT = [K17 * NF2 * MATSW]^{= J_{17}} - [K19 * NF3]^{= J_{19}} - [K20 * NF3 * MATSW]^{= J_{20}}$$


WA
MINT
STG
DR
OUTSIDE POPULATIONS
DENS
4
J21
MON
5
J18
3
J22
NF3
J17
NF2
J20
1
OTHER WADERS
BIOM
NB
J16
J15
2
J6
J19
SUN
J1
J5
J7
MAT SW
NF1
JR
BP
X
J14
J13
J8
NBR
FLG SW
CL
NE NEW
AFR
PFA
NBR NEW
HAT SW
NN
J9
NE
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J2
J3
J4
J10
J12

energy-circuit language and symbols in detail. In short, the symbols and pathway networks represent storages and flows of energy through the system and thus the pathways of causal force actions. The diagramming language is such that the model diagrams can be translated directly into the mathematical equations used in computer simulations of the system. The language is a symbolic form of mathematics, keeps track of energy laws, and is a useful tool for studying the emergent properties of complex systems. The primary components of energy circuit models are external environmental forcing functions (large, labeled circles around right and upper edges), energy and material storages (labeled tear-drop shaped tanks), energy and material flow pathways, interaction work gates (fat arrowheads, sometimes with multiplication and divisor signs within), and threshold switching functions (squares with concave sides). Particular flows in the model are labeled with J# codes (Fig. 6-3). Rate coefficients for each flow (K# values in the flow equations; see legend for Fig. 6-3) are calculated by estimating average flows based on field or literature data and dividing these by appropriate estimates of average upstream storages. Thresholds for switches are also estimated from literature values and field data. A series of differential equations then becomes the basis for simulating changes in each storage over time.

The data and calculations used to derive the rate coefficients for the Great Egret model are summarized in Appendix B. Programming and simulation of the model was accomplished using Microsoft® QuickBASIC v4.5 (readers interested in the program code may contact the author).

In formulating the model, I sought to explicitly recognize the following probable influences:

1) A large expanse of marsh flooded to at least moderate depths from fall into winter ensures the production of large numbers of prey organisms (Loftus and Eklund 1994).

A steady late-winter through spring surface-water recession then ensures consistent access to concentrated prey resources for nesting wading birds (Kushlan et al. 1975; Frederick and Collopy 1989a; Bancroft et al. 1994; Chapters 2, 4). However, a severe reduction in wetland area and excessive concentration of prey organisms may lead to high prey mortality (Kushlan 1976b; Browder 1976) and potentially low recruitment the following year (Loftus and Eklund 1994).

2) Wading bird activity at the lake involves both migratory populations that move outside the southern Florida region--some only nesting at the lake, some only wintering--and at least regionally-resident if not lake-area resident populations that regularly breed in the area (Palmer 1962).

3) During severe drought periods, large lacustrine or deep-pool systems such as Lake Okeechobee serve as regional refuges for wading birds dispersing from dried palustrine systems in the Everglades and surrounding areas (Chapter 2).

4) The responses of breeding adults to fluctuations in climatic and hydrologic forces may differ in annual pattern from those of non-breeding populations, because breeders must rely on long-term environmental cues that help them predict in advance what foraging conditions will be like when their young demand large amounts of food (Chapter 4).

5) Severe climatic events such as a two-year drought may lead to a poor correspondence between levels of reproductive effort and the productivity of successful nests--particularly among larger species with longer nesting cycles--because early-season environmental cues will be unreliable for predicting conditions during the peak brood-rearing period (Chapter 4).

6) Abrupt and extended reversals of otherwise protracted spring surface-water recessions result in rapid dispersal of prey and high rates of nest failure (Bancroft et al. 1994; Frederick and Collopy 1989a; Chapter 5), but slowly and steadily rising water levels that yield accessible, newly-flooded wetland areas may support successful nesting (Chapter 5).

7) During the peak drought year of 1990, Great Egrets turned to panhandling fish scraps to supplement the supply of food they provided to nestlings (Chapter 3, 4).

Prey Population Dynamics

I modeled prey production (labeled as flow J1 in the model) as proportional to the product of: 1) solar energy input (SUN; one of three input variables); 2) an exponential-saturation function (i.e., of the form $y = a * [1 - e^{nx}]$) of relative surface-water area (WA; represented as box 1 in the model diagram, Fig. 6-3); and 3) and autocatalytic feedback loop (Odum 1983) dependent on total prey biomass (BP). I derived the weekly solar energy data from values provided in Browder (1976; 5-year monthly means), which she obtained from the Belle Glade Agricultural Experiment Station located just south of the lake. I then scaled these values as a percentage of an arbitrary maximum (Fig. 6-4). I derived estimates of WA based on output from the OKEEHYDRO hydrologic model described in Richardson and Hamouda (1994). I began with estimates of mean water depth calculated for the 15th and last day of each month, resolved to a spatial scale of 100 m^2, and represented in raster-based GIS map files. I then used a custom program (POLYSTATS, Richardson 1993) to calculate a mean depth for each date for each of 489 1 km^2 transect grid cells that I regularly surveyed for wading birds (Chapter 2). I set the estimates of surface-water area equal to the number of grid cells with a mean depth greater than zero. For modeling

convenience, I derived a linear function to calculate total surface-water area (WAREA in km^2) in the survey region from estimates of weekly-mean lake stage (STG, the second input variable; data provided by the SFWMD; Fig. 6-5). I then scaled WA as the percentage of maximum possible water area (i.e., 489 km^2). I incorporated the nonlinear function for WA (Fig. 6-6) for reasons discussed in the simulation results section.

I incorporated a density-dependent mortality factor (J2) to account for carrying-capacity-control of prey growth, as in standard equations for logistic growth (Browder 1976; Odum 1983). I modeled prey respiration (J3) as a function of relative prey biomass density (BP / WA), because mass-specific respiration rates typically increase as density increases (Browder 1976). I modeled prey mortality due to causes other than wading bird predation (J4) as a function of relative surface-water area (WA), because predation by larger fish and other predators increases as prey and aquatic predators are concentrated in receding pools (Kushlan 1976b; Loftus and Kushlan 1987; Loftus and Eklund 1994), and because the drying of isolated pools may lead to high prey mortality (Browder 1976; Kushlan 1976b).

Chick and McIvor (1994) collected monthly samples of small fishes in two submerged vegetation and two emergent vegetation habitat types in 1990. Bull et al. (1992) collected fall samples in several submerged and emergent vegetation habitat types in 1989 and 1990. I opportunistically collected samples in a wide variety of habitat types in conjunction with observations of foraging birds during 1990 and 1991 (McIvor and Smith 1992; unpubl. data). By combining data from these sources, I

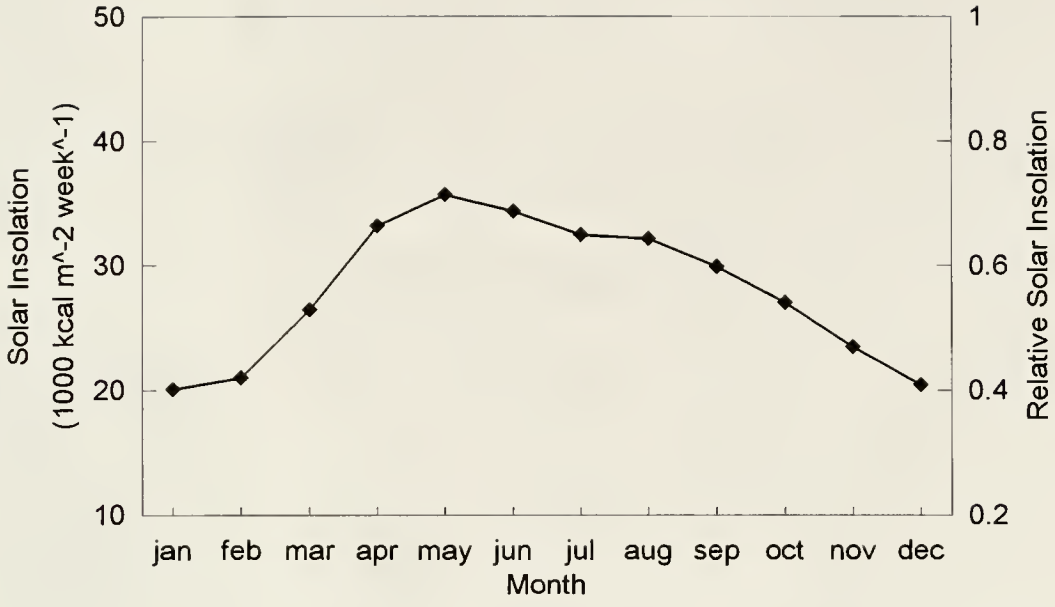

Figure 6-4. Five-year mean weekly solar insolation at Belle Glade, Florida (from Browder 1976).

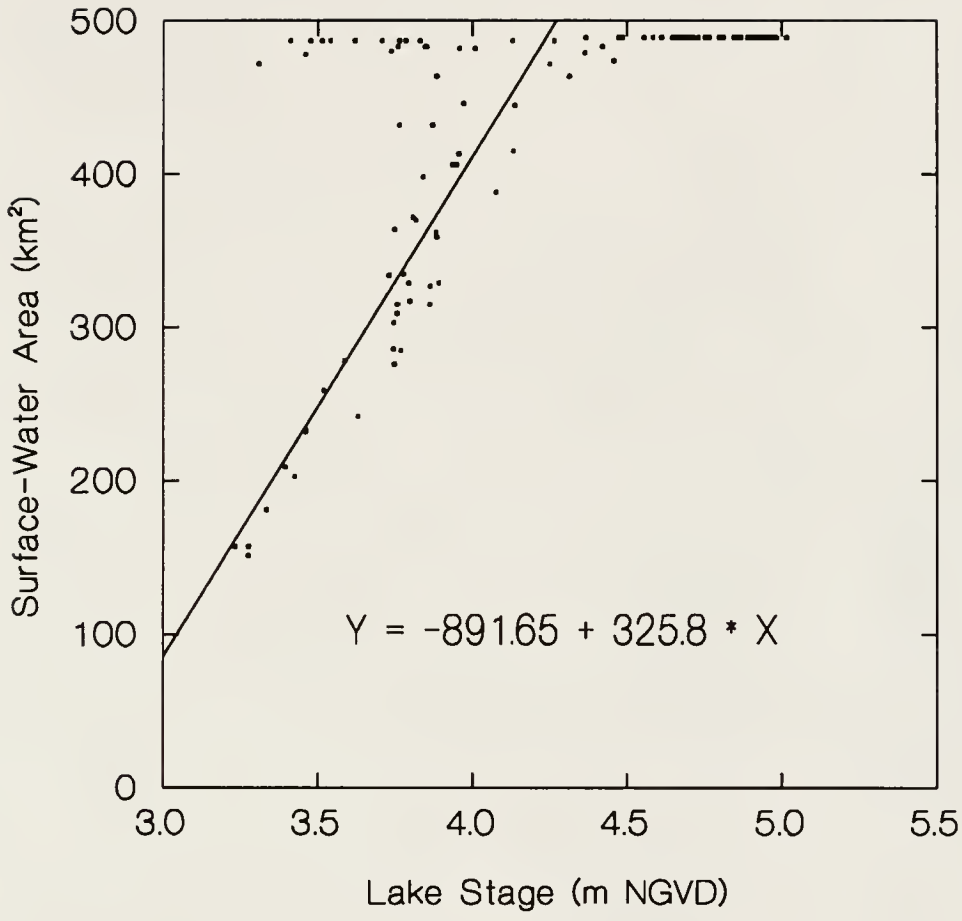

Figure 6-5. Function used in the model to calculate the total surface-water area (WAREA) in the transect survey region from estimates of daily lake stage (STG).

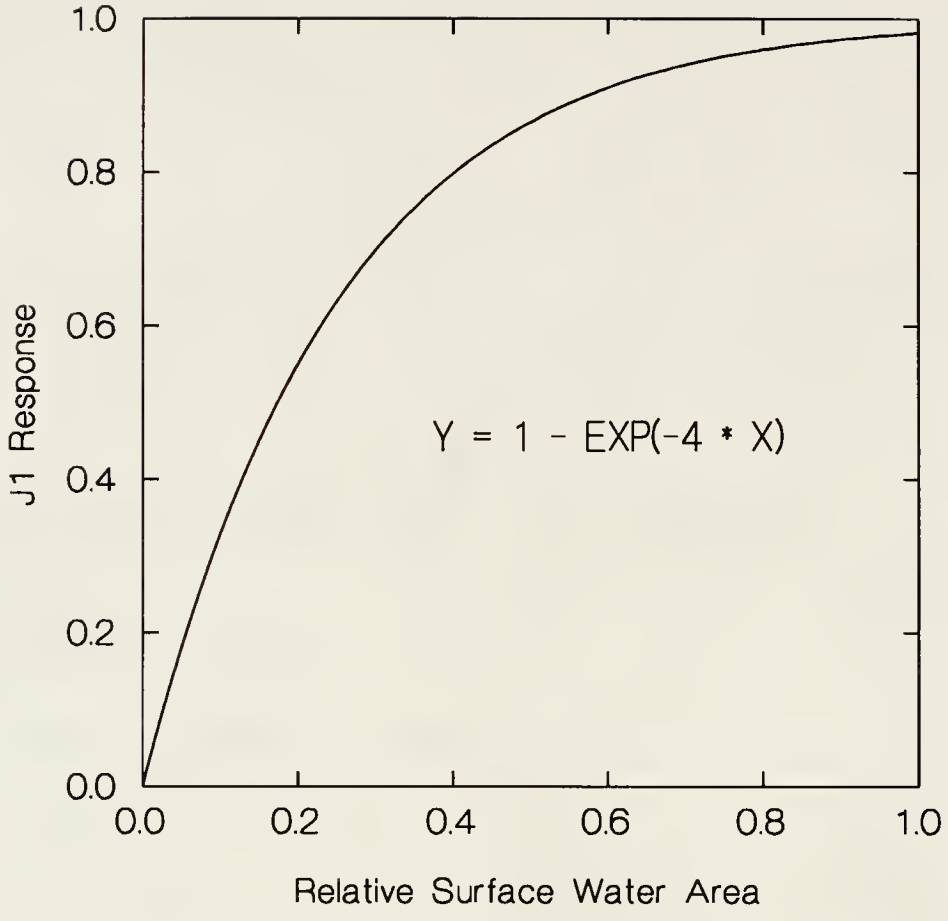

Figure 6-6. Functional response of prey production (J1) to variation in relative surface-water area (WA).

derived a rough estimate (in so far as the data were spatially and temporally sparse) of the lakewide mean density of forage fishes on the lake during the study (18.2 g m^{-2} wet weight). Although Great Egrets regularly forage on organisms other than fish, fish often make up the bulk of their diet (Bent 1926; Palmer 1962; Collopy and Smith 1991). Therefore, for the purpose of deriving the initial rate coefficients, I limited my attention to data for fishes, but then adjusted the rate coefficient during simulation to reflect a higher diversity and abundance of prey. For the purpose of estimating rate coefficients dependent on prey biomass (BP), I assumed birds foraging and nesting in the area could access 1.5 times the area--and therefore prey biomass--available in the survey region. This was a crude approximation to account for the fact that birds could easily gain access on a day-to-day basis to other areas on and immediately adjacent to the lake. Otherwise, I used estimates of prey growth, respiration, and mortality provided in Browder (1976; adjusted to reflect wet weight rather than dry weight) to back-calculate the K1-K4 rate coefficients. Browder's data were derived from sampling conducted in a pond and adjacent emergent marsh area within the Corkscrew Swamp Sanctuary located 60-70 miles southwest of Lake Okeechobee in Collier County.

Prey Consumption by Wading Birds

I modeled prey consumption by Great Egrets (J5) as the product of: 1) a logarithmic function of relative prey biomass density (BP / WA; Browder 1976); 2) a linear function of the surface-water drying rate (DR); 3) an exponential-sigmoid function (i.e., of the form $y = a / [1 + b * e^{nx}]$) of weekly-average minimum daily air temperature (MINT; the final input variable); and 4) an autocatalytic positive feedback loop dependent on the number of adults, nestlings, and newly-laid eggs. The first three functions are represented as box 2 in the model diagram (Fig. 6-3). Several studies

have indicated that wading bird prey intake is primarily a function of prey density rather than overall prey abundance (Kahl 1964; Kushlan 1976b, 1978a; Browder 1976; Ogden et al. 1976; Draulans 1987). As Browder (1976) found, the logarithmic function helped stabilize the model and prevent over-feeding. I added the surface-water drying-rate (DR) response because simulations suggested that it produced a closer fit to the observed trends (discussed further in simulation results section), and because wading birds are probably able to associate changes in surface-water levels with changes in foraging conditions and adjust their habitat selection strategy accordingly (Kushlan 1986a). The function was such that receding water encouraged greater immigration (response > 1) and rising water reduced immigration (response < 1). I added a minimum temperature (MINT) response because small fish activity levels decline during cold weather, a factor that reduces the foraging efficiency of wading birds and leads to increasing nest failure (Frederick and Loftus 1993; Chapter 5). I incorporated the nonlinear function (Fig. 6-7) for reasons described in the simulation results section. The autocatalytic feedback loop was appropriate because wading birds often rely on local enhancement and information exchange at the colony to increase their chances of finding rich food sources (Chapter 3; Ward and Zahavi 1973; Ogden 1978b; Kushlan 1981; Erwin 1983). Moreover, the production of eggs and especially the hatching of nestlings elicits increased foraging activity and intensity among breeding adults (Erwin 1985).

I derived the J5 rate coefficient (K5) by assuming an average flow of biomass equal to the maintenance needs of 2,200 adults, the average food requirements of 600 nestlings, and the biomass sufficient to produce 100 new eggs (at 27.4 g egg^{-1}, estimated from hatching-day measurements of nestlings; unpubl. data). The number of adults was an average based on survey counts. The nestling and egg numbers were

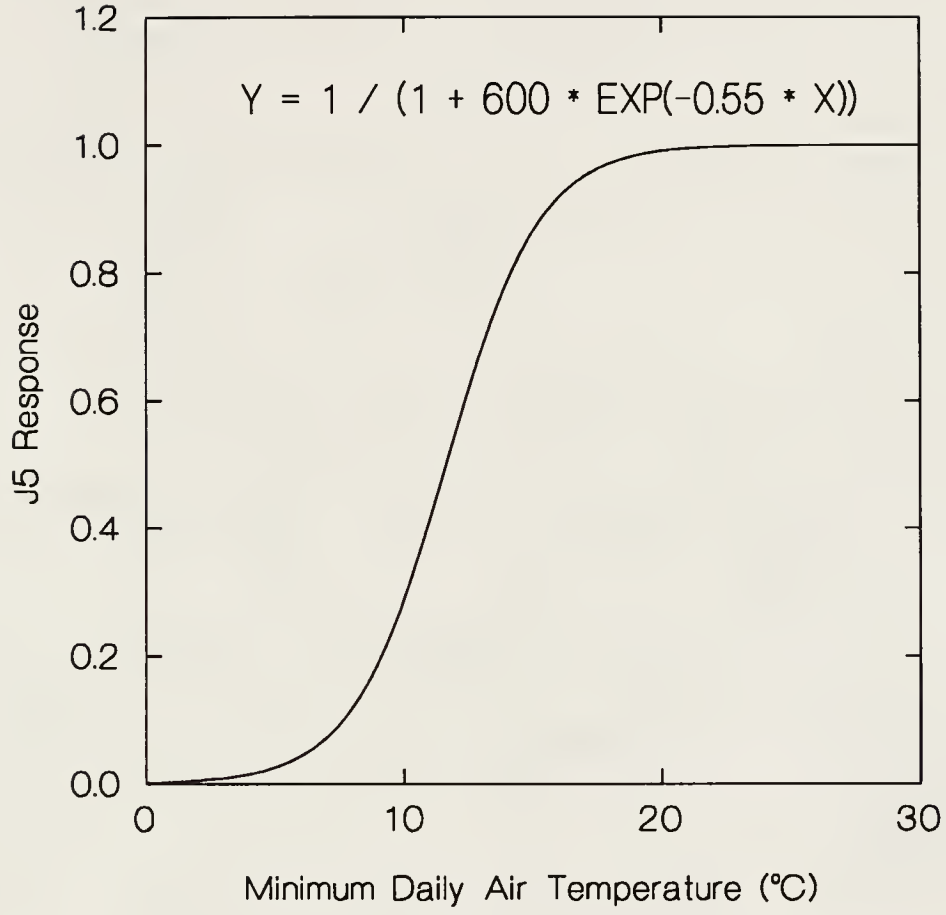

Figure 6-7. Functional response of Great Egret prey consumption rate (J5) to variation in minimum daily air temperature (MINT).

reasonable but comparatively arbitrary estimates. I derived the estimate of adult maintenance needs by assuming an average adult mass of 1,000 g and using the regression equation provided in Kushlan (1978a): log y = 0.966 log x - 0.640, with y = daily food requirement in grams and x = bird mass in grams. Palmer (1962) gives a mass for one Florida female of 917 g, and measurements I took on nestlings at the lake (unpubl. data) indicated a maximum mass of 1,050 g, with outwardly healthy 30-40 day old young typically weighing from 900-1,000 g. The resulting estimate was a daily food requirement of 181 g per adult. I estimated the average nestling food requirement based on information in Mock et al. (1987; a daily mean of 71.9 g food fed to three-chick broods during the first 25 days) and the assumption that nestling food requirements approached those of the average adult by 30 days. The result was an estimate of 117 g food per nestling per day over the 9 week rearing period.

I modeled the consumption of prey by non-Great Egret wading birds (J6) as proportional to Great Egret consumption (J5). The proportionality constant (B6) equaled the product of the mean ratio of non-Great Egrets to Great Egrets derived from count surveys (Chapter 2) and an energy-needs reduction factor calculated to account for the fact that the bulk of the other wading birds at the lake were species smaller than Great Egrets. I calculated the relative energy needs of species of different mass from the regression equation provided by Kushlan (1978a).

Great Egret Immigration and Emigration

I modeled the immigration rate (J22) as primarily a function of prey biomass density and the surface-water drying rate (DR). Because it made fitting the function much easier, I based the density function on estimates of actual prey biomass density (DENS), rather than the relative function (BP / WA) incorporated elsewhere. The model

calculated DENS as BP divided by 1.5 times the estimated surface water area (m^2) in the survey region. I modeled the DENS effect as a sigmoidal response that reached an asymptote of one at 4-5 times average density (Fig. 6-8). The DR effect operated as it did on J5. I also made the immigration rate a function of lake stage (STG)--an exponential increase in the immigration rate at low stages (Fig. 6-9)--to account for the drought-refuge response eluded to above. I set the minimum value as 0.35, because even at high lake stages some birds forage on the lake. I also added a local-enhancement effect by allowing the number of birds already foraging on the lake (NB) to exert additional multiplicative control, but incorporated a maxima function (i.e., of the form $y = a*x*e^{nx}$) to prevent overcrowding and did not allow a lack of birds to reduce the immigration rate below that indicated by the other factors (response ranging from 1-1.5; Fig. 6-10). The above combination of influences is represented as box 5 in the model diagram (Fig. 6-3).

For the purpose of this model, I assumed that the pool of potential immigrants was unlimited, and in the model the immigration rate was calculated as a percentage--the product of the above functions--of a maximum rate (i.e., essentially the K22 coefficient). In contrast, the emigration rate (J21) was necessarily proportional to the number of birds present (NB). Otherwise, I modeled the emigration rate as a function of the sum of prey biomass density (DENS) and surface-water drying rate (DR) effects. I represented the DENS and DR effects as sigmoidal functions, with declining density and rising water each eliciting increased emigration, with an asymptotic maximum response of 0.5 (i.e., at maximum influence, each variable would cause 50% of the birds to leave per week; Figs. 6-11 and 6-12, respectively). The K21 rate coefficient was, therefore, irrelevant and set at one. The combination of functions influencing the emigration rate is represented as box 4 in the model diagram (Fig. 6-3).

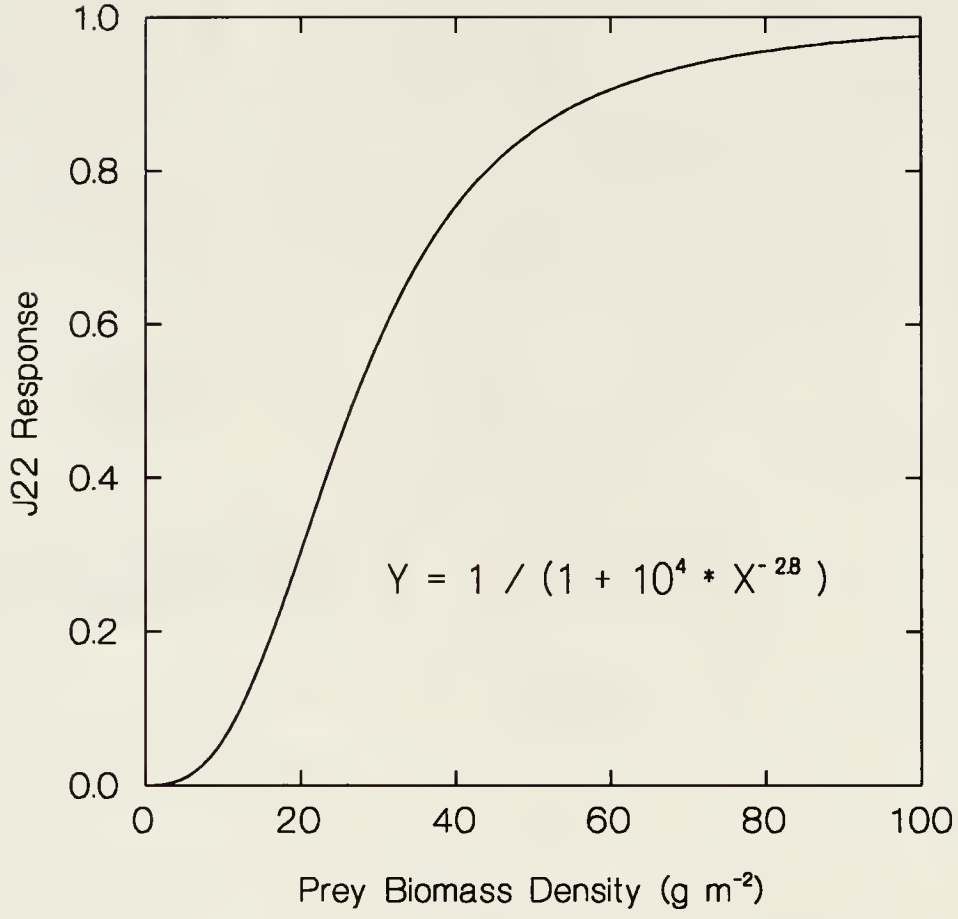

Figure 6-8. Functional response of Great Egret immigration rate (J22) to variation in prey biomass density (DENS).

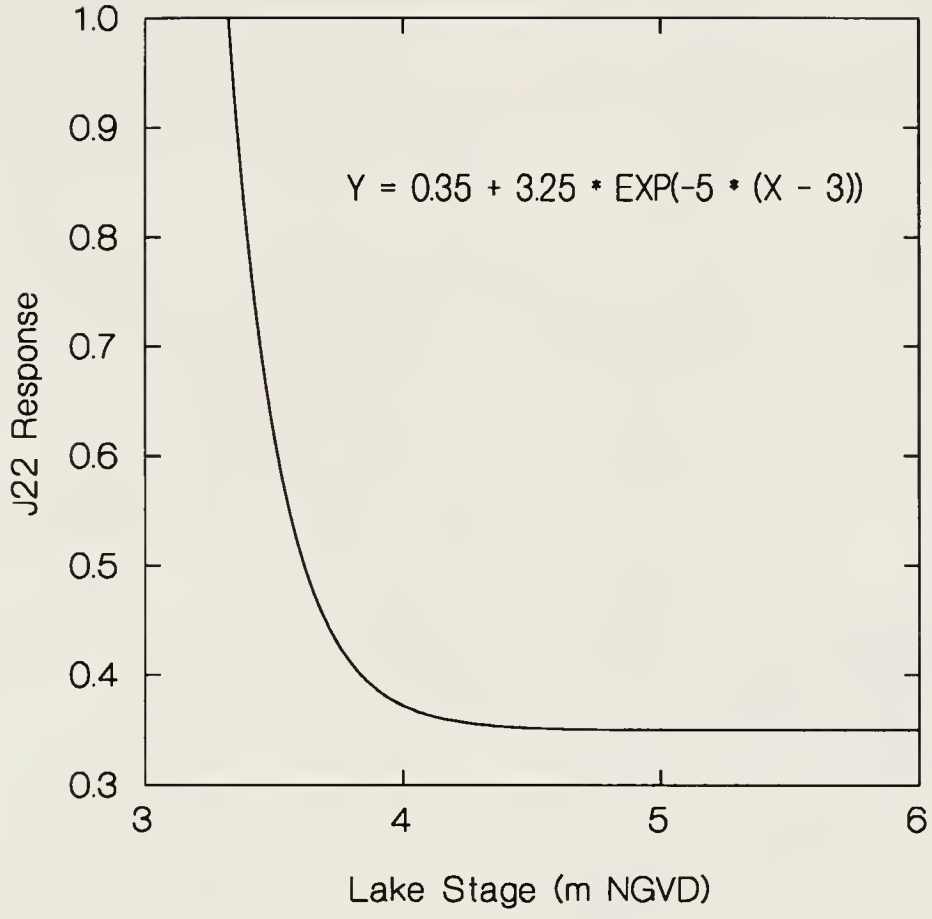

Figure 6-9. Functional response of Great Egret immigration rate (J22) to variation in daily lake stage (STG).

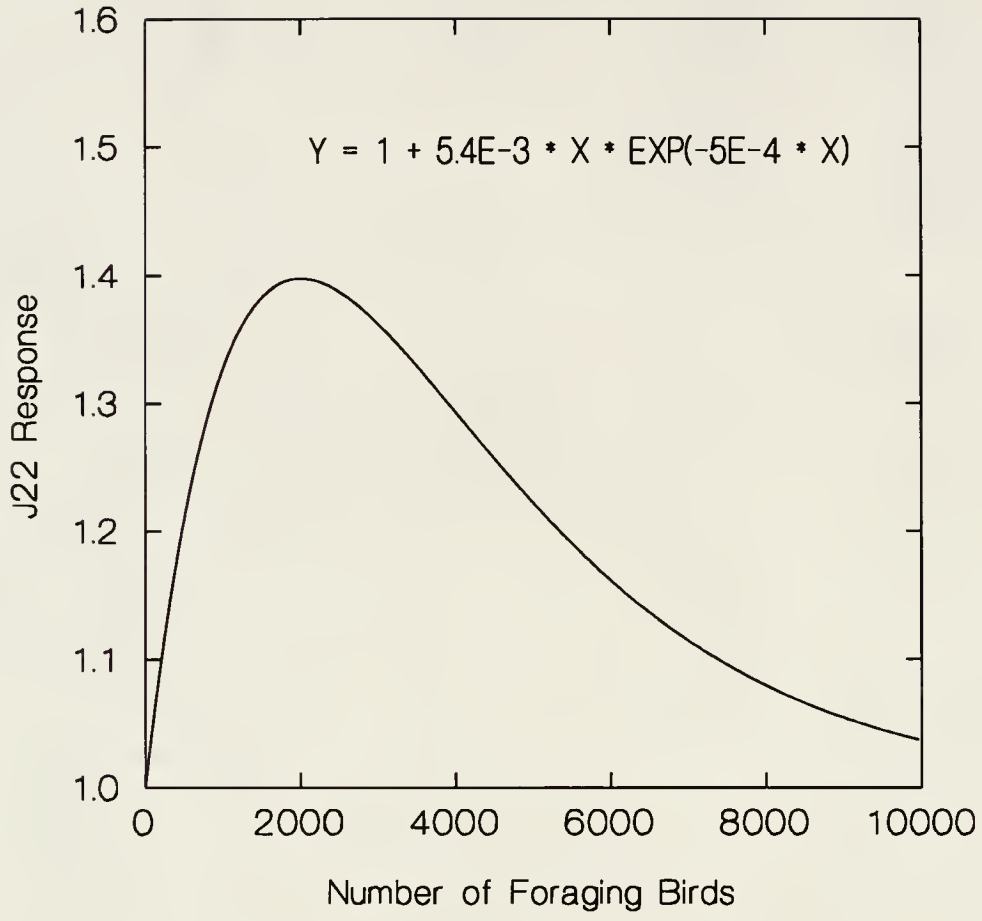

Figure 6-10. Functional response of Great Egret immigration rate (J22) to variation in the number of foraging birds already at the lake (NB).

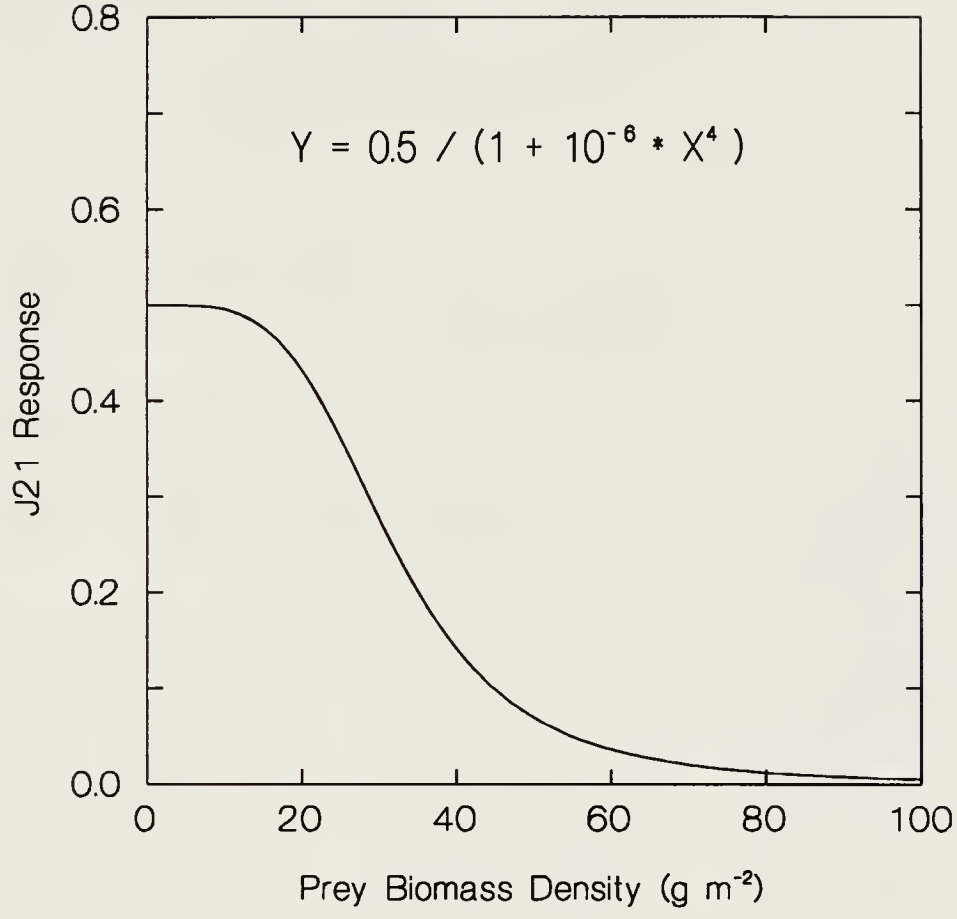

Figure 6-11. Functional response of Great Egret emigration rate (J21) to variation in prey biomass density (DENS).

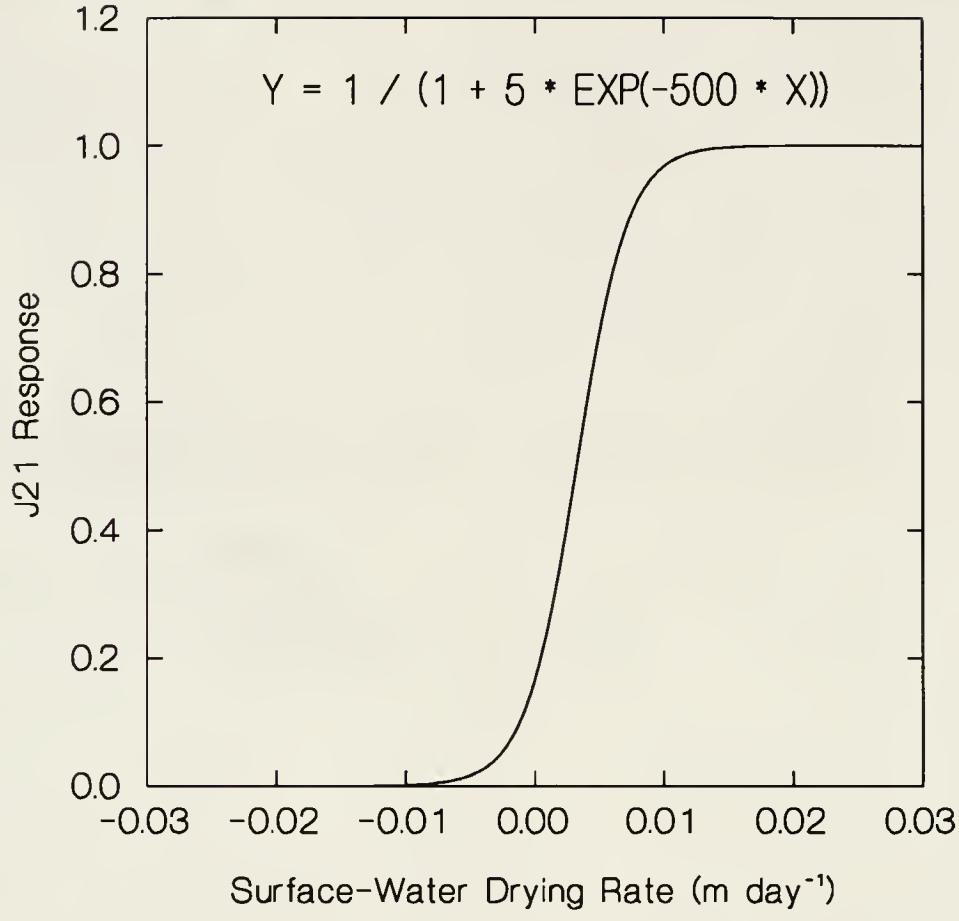

Figure 6-12. Functional response of Great Egret emigration rate (J21) to variation in the surface-water drying rate (DR).

Recruitment of Breeding Birds and Reproductive Dynamics

Primary control of breeder recruitment occurred through a truncated inverse cosine function of date (MON), which prevented the initiation of new nests from mid-May through mid-December and encouraged peak nesting effort from mid-February through mid-April (Fig. 6-13). The cutoff dates roughly corresponded to the earliest and latest dates on which I found eggs during the study. Otherwise, I modeled the recruitment of breeders as proportional to the total number of birds in the area (NB) and secondarily as a nonlinear function of lake stage (STG). As discussed above, Great Egrets initiated the most nests in years that began with relatively high winter water levels. To reflect this tendency, I controlled the rate of nest initiation through an exponential-sigmoid function of lake stage, with maximum initiations at stages above 4.5 m and minimum initiations at stages below 3.5 m (Fig. 6-14). The combination of MON and STG functions is represented by box 3 in the model diagram (Fig. 6-3).

The breeding adult storage (NBR) is shown in Figure 6-3 with no outflows except the contribution to egg laying. At each iteration of the model, an expected number of breeders was calculated based on the above functions and the abundance of foraging birds on the lake at the time. The expected value at time t - 1 was then subtracted from the value at time t to yield the number of new initiations (NBRNEW), if any. The number of eggs laid during the current iteration then became the product of half the number of NBRNEW (i.e., the number of pairs) and the mean clutch size (CL) observed during the study (2.9). The NBR storage therefore was distinguished only for purposes of calculating the number of new eggs, and was not treated as an independent storage with balancing inflows and outflows.

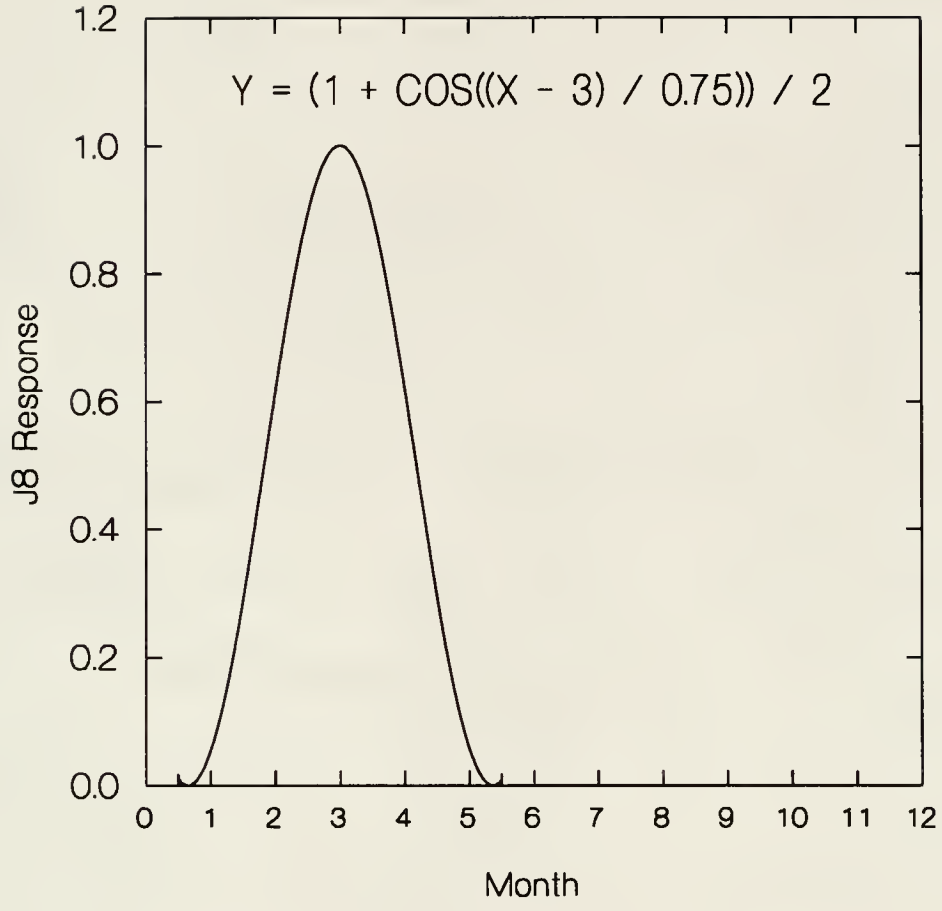

Figure 6-13. Functional response of Great Egret breeder recruitment rate (J8) to change of season (MON). Response is truncated as shown by logical functions in model.

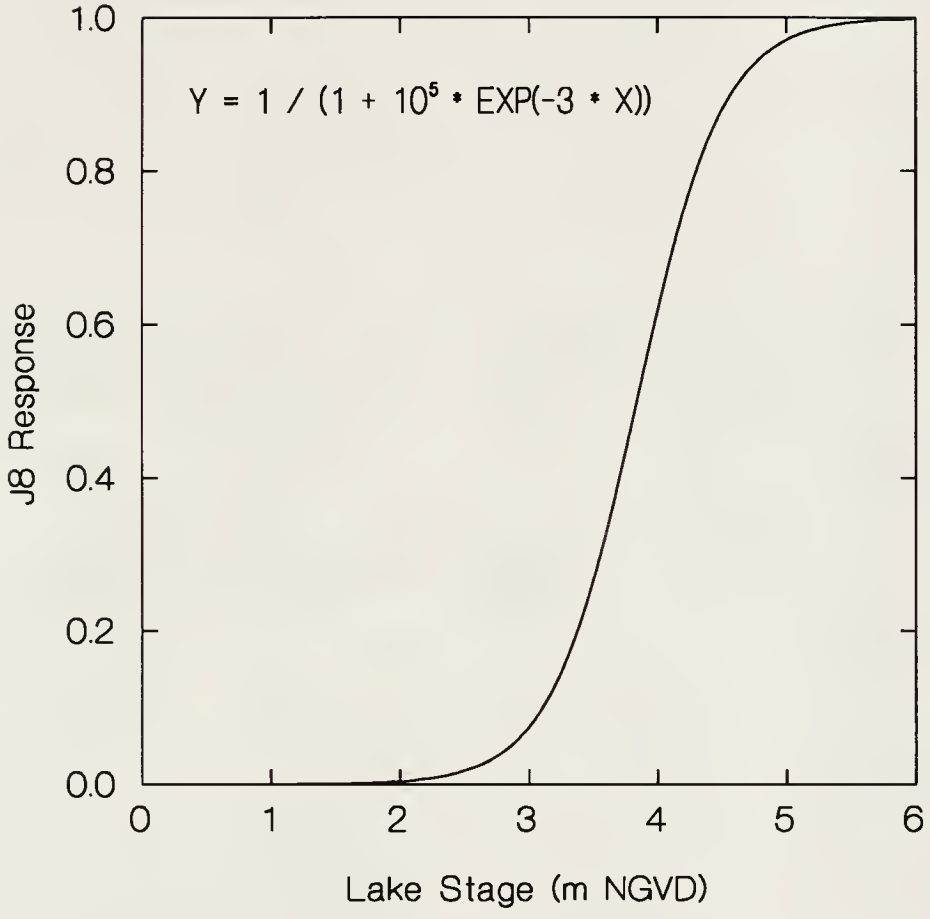

Figure 6-14. Functional response of Great Egret breeder recruitment rate (J8) to variation in daily lake stage (STG).

I included separate egg (NE) and nestling (NN) storage tanks in the model, because adults require less food during the incubation phase than during the brood-rearing phase, and the responses to changing foraging conditions therefore may differ (Chapter 5). I added a time-lag switch (HATSW) to prevent hatching (J11) until 4 weeks beyond the laying of the first eggs each season (the average incubation period for the species is 26-28 days; Wiese 1975; unpubl. data). A similar switch (FLGSW) kept nestlings from fledging (J13) until 9 weeks beyond the time the first eggs hatched (Wiese [1975] determined the average age at fledging to be 62-70 days). Hatching and fledging rates (J11 and J13, respectively) and the associated loss rates (J10 and J12) were linear functions of the amount of prey secured by foraging adults (PFA). PFA equaled the current J5 divided by AFR, with AFR equal to the current maintenance-level food requirements of the adults present (estimated as above). I estimated the mortality and survival rate coefficients (K10 - K13; see Fig. 6-3) based on the survival levels observed during the study (53% of eggs hatched, 58% of hatched eggs to fledging). Egg loss (J10) increased and hatching (J11) decreased (i.e., nest abandonment increased) if the flow of prey to adults fell below 1.3 times the estimated AFR (PFA < 1.3). I adopted the factor of 1.3 to approximate the extra energy demands of incubation. I estimated the average daily total food requirement for a single nesting adult and its nestlings at 321 g, which equaled the 181 g maintenance needs of an adult plus half the 117 g $bird^{-1}$ needs of 2.4 nestlings (during this study the mean brood size at hatch equaled 2.6, and then declined to 2.2 by 21 days; unpubl. data). Accordingly, in the model nestling mortality (J12) increased and fledging (J13) decreased if PFA dropped below 1.8, and decreased if prey flow increased beyond this threshold.

No definitive data are available concerning the age at which Great Egrets enter the breeding population. Palmer (1962) cites a statement by Morton that maturity is attained at three years, and Kahl (1963) assumed that most individuals do not breed until they exceed two years of age. In the model, a maturation switch (MATSW) operated at the beginning of December, prior to the new breeding season, to shift subadult birds between age categories. NF1 birds represented fledglings less than one year old, NF2 birds represented subadults between one and two years old, and NF3 birds represented subadults between two and three years old. At maturation time, all of the surviving NF3 birds and 40% of the surviving NF2 birds were recruited to the adult pool of potential breeders (flows J18 and J20, respectively). The other 60% of the NF2 birds became the new pool of NF3 non-breeding subadults (J17), and all the surviving NF1 birds became the new pool of non-breeding NF2 subadults (J15). Kahl (1963) estimated from 15 years of band return data that Great Egret mortality averaged 76% in the first year following fledging, and then dropped to an average of 26% in subsequent years. These mortality levels were based on a year beginning July 1. Therefore, in the model I set the average NF1 mortality rate (K14) at 0.76 / 52 weeks = 1.46% of the birds present per week; the NF2 mortality rate (K16) at ((0.76 + 0.26) / 2) / 52 = 0.98% per week; and the NF3 (K19) and adult (K7) mortality rates at 0.26 / 52 = 0.50% per week.

For purposes of tracking prey consumption and biomass transfers, I ignored fledglings and subadults. In other words, I assumed that all fledglings dispersed from the lake and returned only when they were ready to breed. This is not entirely accurate, but fledglings often disperse widely during their first fall (Palmer 1962) and the number of subadults consuming prey was probably always small compared to the total number of birds foraging on the lake. I also assumed that all nestlings that

reached maturity returned to breed at the lake, but this may not be a valid assumption either. I color-banded 21 Great Egret nestlings in 1989 and 107 in 1990 that fledged successfully. If the mortality levels indicated by Kahl (1963) pertained, 28 of the banded 1989 and 1990 fledglings would have survived to potentially breed at two years of age. I never observed a banded adult in the colonies, but two banded Great Egrets were seen in the area during the year following their birth. No other information is available concerning levels of philopatry in this species.

Simulation Results and Discussion

Prey Population Dynamics

Figure 6-15 displays the standard simulation output of total prey biomass (BP) and prey biomass density (DENS) in relation to trends in solar energy input (SUN), relative surface-water area (WA), and lake stage (STG)--i.e., the primary external forcing functions. Fluctuations in solar input controlled the production of prey at moderate to high lake stages, but water area became the dominant controlling force at lower lake stages, with total prey biomass reduced dramatically at low lake stages during the drought. In contrast, prey density followed generally the same trends as total prey biomass at higher lake stages, but increased as the relative surface-water area (WA) declined. The result was that prey density largely followed the trend in solar input, but was lowest in 1988 and 1992 with the highest lake stages. Densities probably were even lower in 1988 and 1992 at high lake stages, because the model did not directly account for the influence of water depth. At high stages vegetative cover declines, because water depths become too deep for many emergent and submergent species to thrive (Pesnell and Brown 1977; Richardson and Harris 1994). This would in

turn reduce the productivity of small fishes and macroinvertebrates, because such species depend on food sources associated with vegetation and on the protection from aquatic predators that dense vegetation provides (Werner et al. 1977; Chick 1992).

In the model, relative surface-water area (WA) influenced prey production through an exponential-saturation function (Fig. 6-3). Substituting a linear effect (i.e., J1 = K1 * JR * BP * WA instead of J1 = K1 * JR * BP * 1 - EXP[-4 * WA]) produced a very different simulation response pattern than that shown in Fig. 6-15, with prey biomass and density following similar trends (Fig. 6-16). The latter pattern was not consistent with prey sampling results. Prey density increased by up to 10-fold in submerged vegetation in Fisheating Bay at the height of the drought in 1990 (Fig. 6-17; data provided by J. H. Chick and C. C. McIvor). Most upper-elevation emergent-marsh habitats were dry at this time (hence the total lack of prey in Eleocharis; Fig. 6-17), and foraging activity therefore was largely restricted to outer littoral zone habitats (Chapter 2). Lake Okeechobee is a large lake with a relatively deep central pool. As long as the drying rate is not too rapid, prey organisms that otherwise would occupy upper-elevation habitats can migrate to outer fringe areas during drought periods and find refuge that is not available to organisms in shallow, isolated palustrine habitats. Thus, large-scale mortality due to habitat desiccation--explicitly included in Browder's (1976) model for Wood Storks--may not occur, and fecundity may not be greatly affected. The resulting high concentration of prey in relatively small areas of submerged vegetation would then serve as a very strong attractor for foraging wading birds.

The nonlinear function for the water area (WA) effect on prey production (J1) meant that the negative impact of declining surface-water area increased slowly at first and rapidly only at very low lake stages (Fig. 6-6). In contrast, prey mortality not due to wading birds (J4) was a linear function of WA, and prey respiration (J3) was a linear

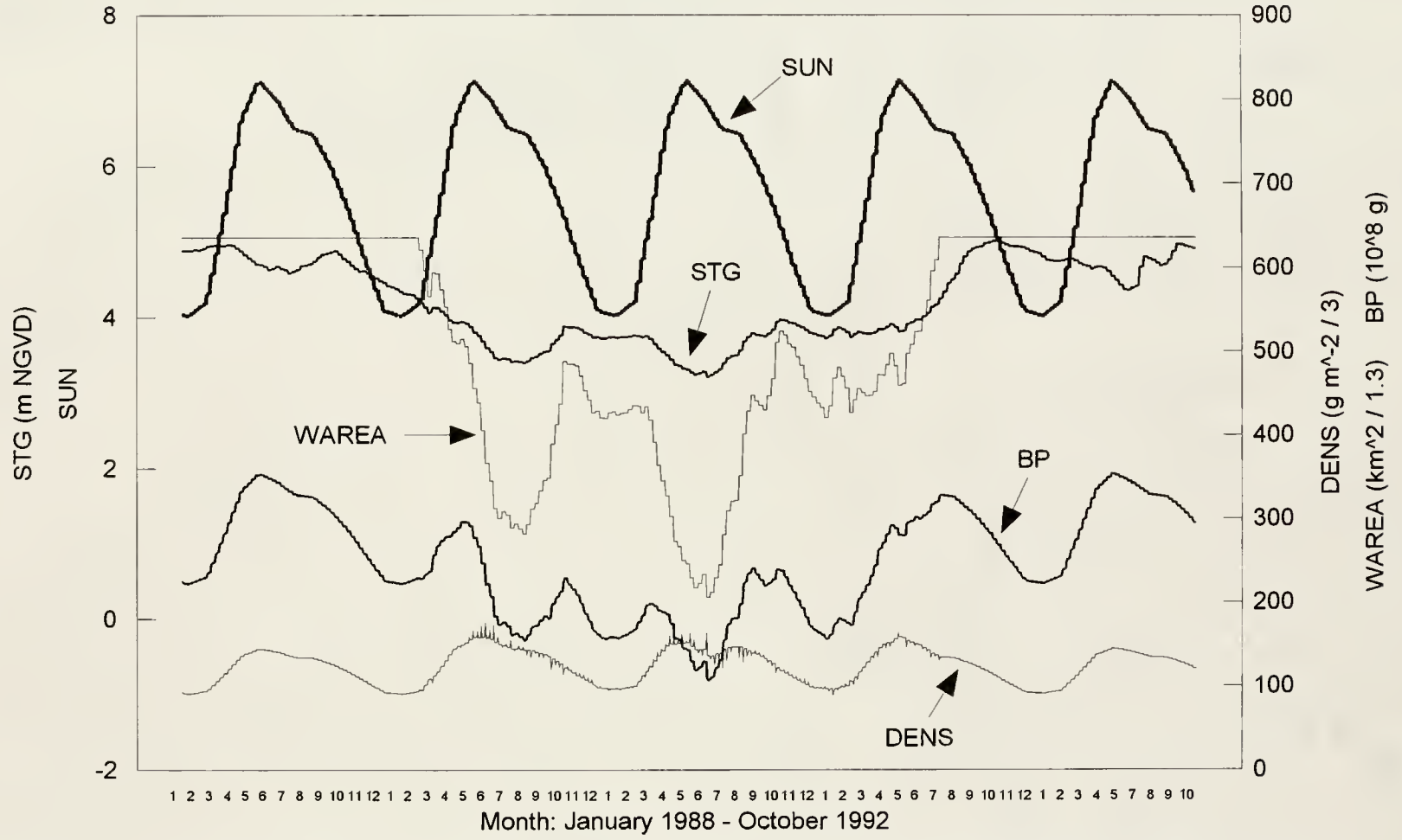

Figure 6-15. Standard simulation output of total prey biomass (BP) and prey biomass density (DENS) in realtion to primary forcing functions: SUN - proportion of maximum mean weekly solar insolation; STG - daily lake stage; WAREA - total surface-water area in primary survey region.

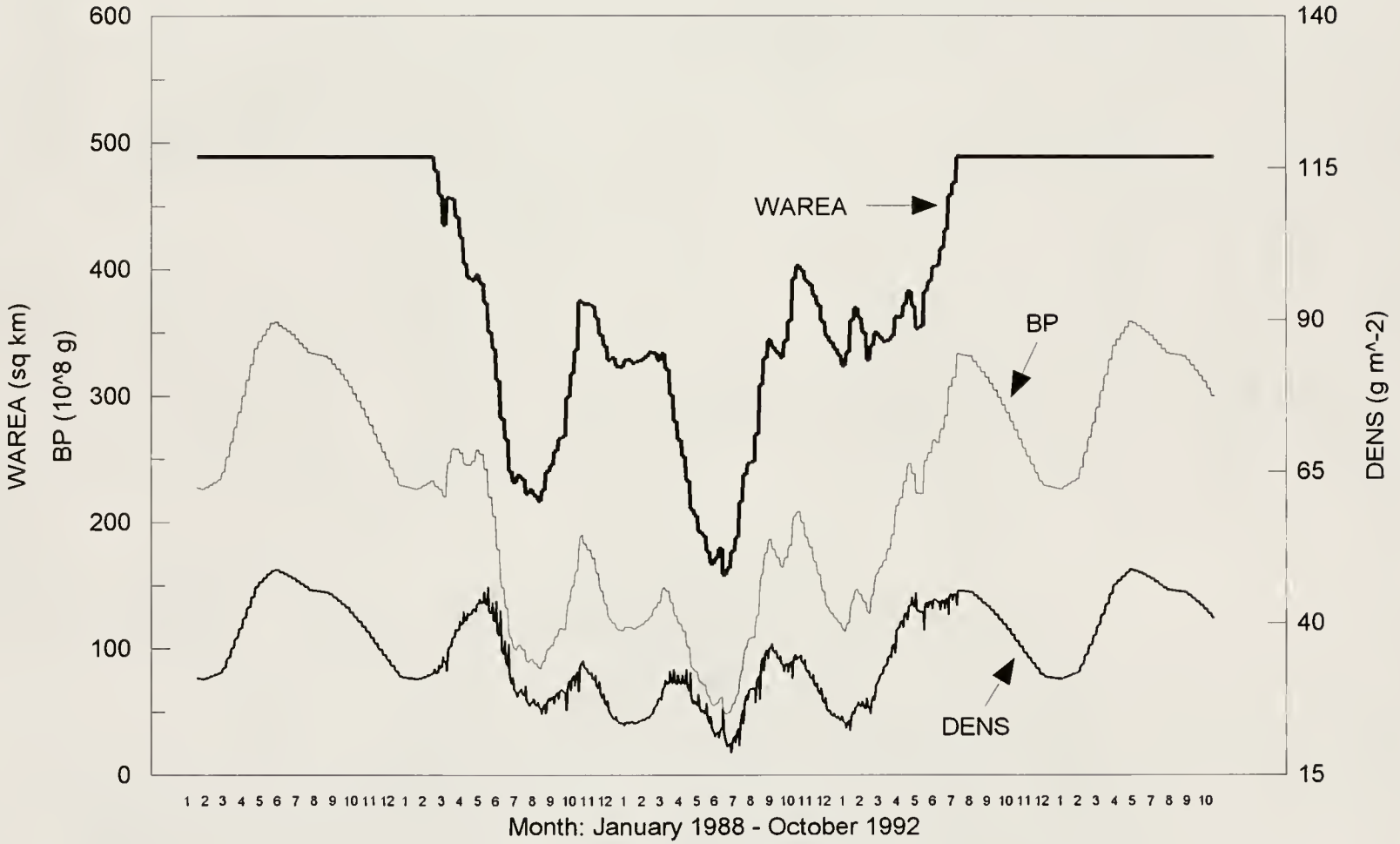

Figure 6-16. Simulation output of total prey biomass (BP) and prey biomass density (DENS) illustrating effect of linear surface-water area factor (WAREA or WA) on prey production (J1).

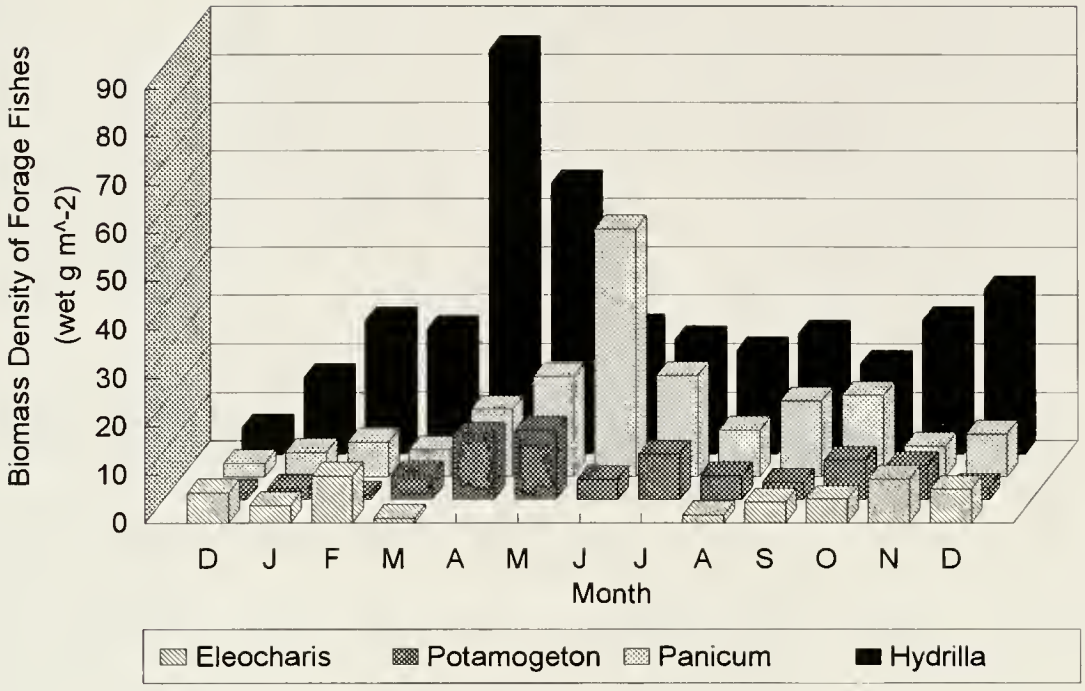

Figure 6-17. Monthly mean biomass density of small forage fishes (<100 mm SL) in four macrophyte types in the west-central littoral zone of Lake Okeechobee from December 1989 through December 1990 (data provided by J. H. Chick and C. C. McIvor).

function of relative prey biomass density (BP / WA). The density effect on prey respiration also produced a strong reduction in net productivity as WA declined and prey were concentrated by the drought. Allowing both J1 and J3 to be strongly affected by declining surface-water area by incorporating the linear effect of WA on J1 doubled the impact and produced the unrealistic response shown in Figure 6-16. Essentially, this was the same problem encountered by Browder (1976) when she allowed prey density rather than just total prey biomass to influence the density-dependent prey mortality rate (J2 in my model). A linear WA function for the J1 response produced reasonable output only if the respiration rate was made a function of just BP or BP^2, not BP * BP/WA. In theory, both prey respiration (J3) and density-dependent mortality (J2) should be modeled as functions of prey density--and therefore water area--not total prey biomass. The question for future study is therefore, which is the best way to model the effects of declining water area? Does it reduce net prey production by reducing fecundity, or by increasing respiration, or by increasing adult mortality, or do all three factors apply but not all to the maximum degree that linear functions allow? It seems most probable that a combination of reduced fecundity and adult mortality are the primary factors. It may also be true that prey production, respiration, and density-dependent mortality should all be modeled as nonlinear functions of water area.

Foraging-Bird Population Dynamics

Figure 6-18 shows the standard simulation results for adult bird abundance (NB) in relation to lake stage (STG) and prey biomass density (DENS). In the model, the number of birds foraging on the lake was primarily a function of immigration (J22) and emigration (J21) rates, and to a much lesser degree recruitment (J18 and J20)(Fig. 6-3). I began by modeling the immigration and emigration responses as functions of only

DENS, but this did not adequately reproduce trends observed in the field (compare Figs. 6-1a and 6-19). Adding the drying rate (DR) effect was the factor most necessary to produce the response shown in Figure 6-18 as opposed to that shown in Figure 6-19. Specifically, the DR effect produced greater net immigration early in 1989 in response to the decline in lake stage that followed the initiation of a two-year drought, and reduced immigration in 1991 when no protracted recession occurred. This suggested that either the prey densities calculated in the model did not adequately reflect the concentration effects of receding water, or that the observed population trends were the result of responses to localized variation in prey density rather than lakewide average densities. During periods of surface-water recession, prey organisms are probably most concentrated at the receding edge where displacement is occurring. Similarly, small fishes may collect along shallow upper margins when water levels are rising to feed on displaced terrestrial organisms and hatching aquatic insects, and amphibian eggs frequently hatch in great numbers in newly flooded areas and attract wading birds (pers. observ.). Such responses would lead to an uneven distribution of prey and might elicit strong responses among wading birds, but lakewide-average prey densities might not change to a degree that would lead one to predict such strong responses.

Initially, I programmed the immigration and emigration rates as simple linear functions of prey biomass density (DENS), the number of birds present (NB), and lake stage (STG). However, as was true for prey production, incorporating nonlinear--primarily asymptotic--functions resulted in simulated responses that more closely matched the trends observed at the lake. The NB local-enhancement effect was relatively unimportant in terms of its effect on the resulting trends. It simply accelerated the rate of immigration when other factors also encouraged immigration; however, a

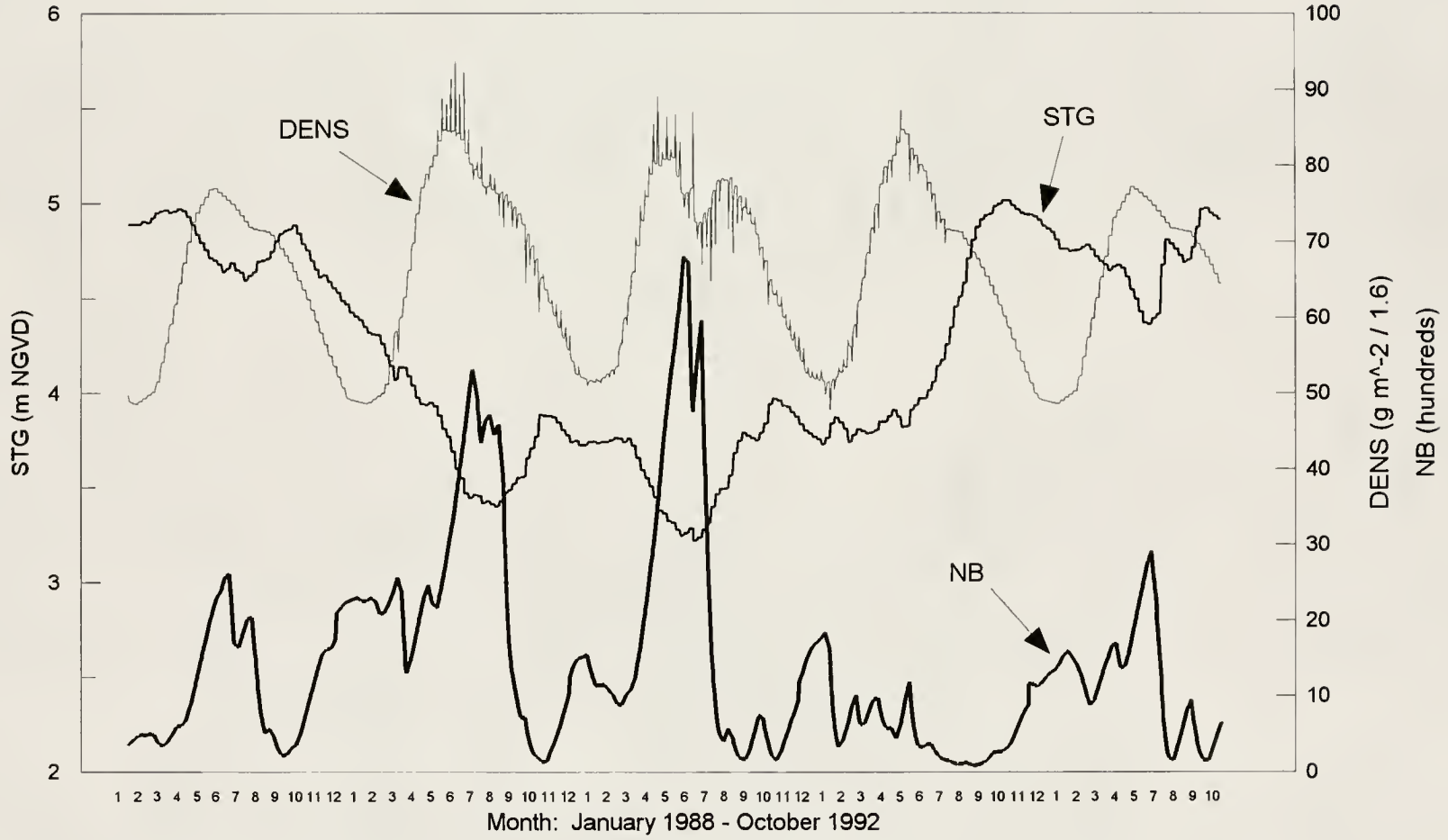

Figure 6-18. Standard simulation output of foraging bird numbers (NB) in relation to prey biomass density (DENS) and lake stage (STG).

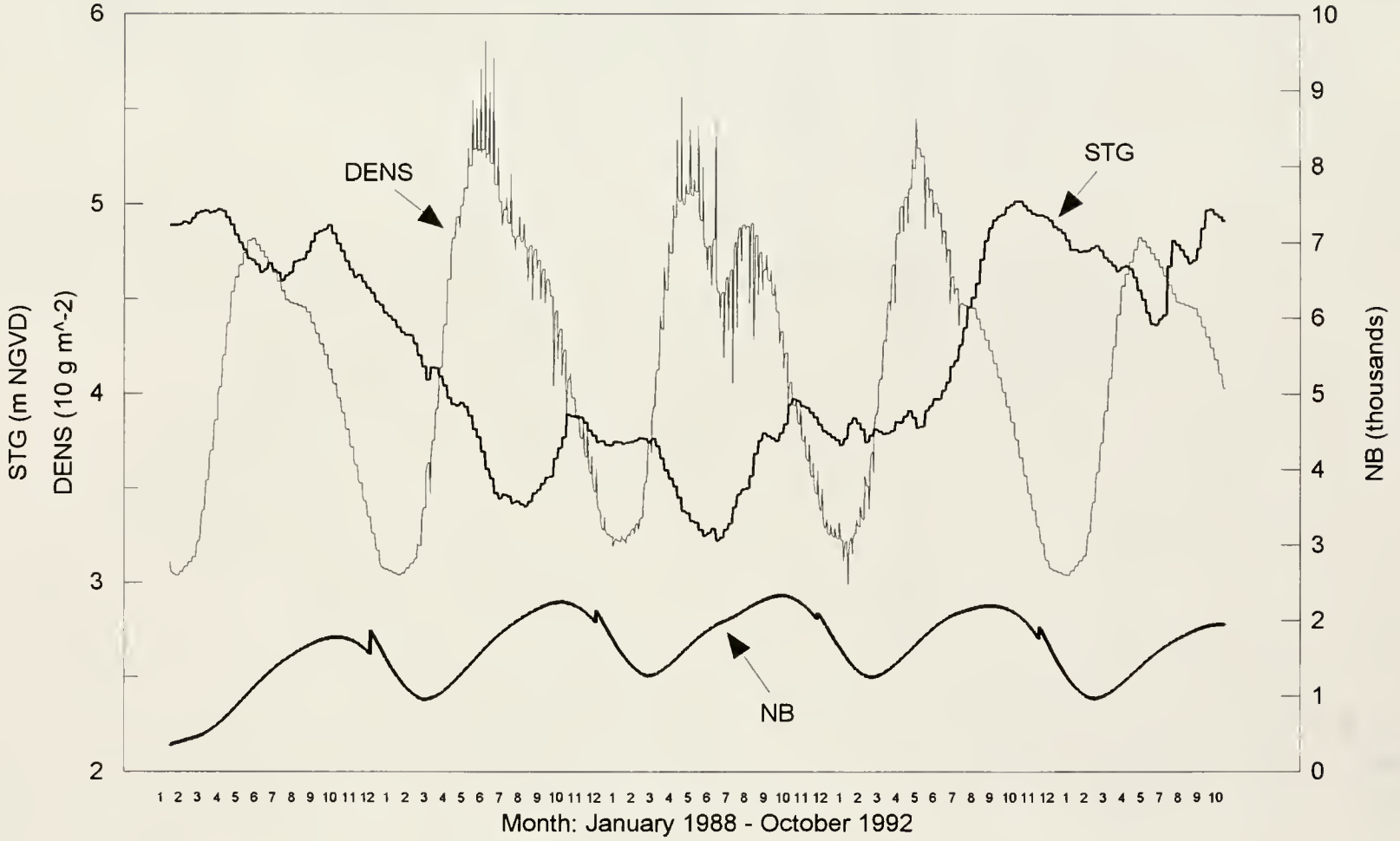

Figure 6-19. Simulation output of the number of foraging birds (NB) illustrating effect of modelling immigration (J23) and emigration (J22) rates as functions of only prey biomass density (DENS). Plot of lake stage (STG) included for reference.

linear response led to out-of-control increases. The STG response was also relatively unimportant compared to the influence of DENS and DR; it simply encouraged a proportionately higher NB peak in 1990, which was consistent with observations. A linear STG response produced generally higher NB throughout 1989-1991, which did not match the observed trends. The difference in simulation results with linear and nonlinear DENS responses was not great, but the asymptotic function helped reduce the degree of fluctuation in the simulated trends.

Recruitment of subadults (NF2 and NF3) to adults (NB) occurred through an abrupt maturation switch (MATSW) at the beginning of December. This in turn produced unrealistically abrupt jumps in NB (noticeable in Fig. 6-20), but the numbers involved were usually small compared the total number of birds foraging on the lake. In reality, maturing subadults would have been part of the overall population all along (although probably not always resident at the lake) and would either have gradually entered the breeding population as they matured, or conversely they may never have settled at the lake if foraging conditions were poor.

Recruitment of Breeding Birds

The standard simulation results for reproductive and recruitment segments of the Great Egret population (NBR, NN, NF1, NF2, and NF3) are shown in Figure 6-20 in relation to trends in the total adult population (NB), lake stage (STG) and prey biomass density (DENS). Initially, I hypothesized that prey density and hydrologic trends might suffice to control the timing of nesting, but discovered that a seasonal control was necessary to reflect the observed patterns of nesting. This was consistent with the results of the logistic regression analysis, which indicated that date-of-initiation was a prominent determinant of the probability of nest failure despite the concurrent

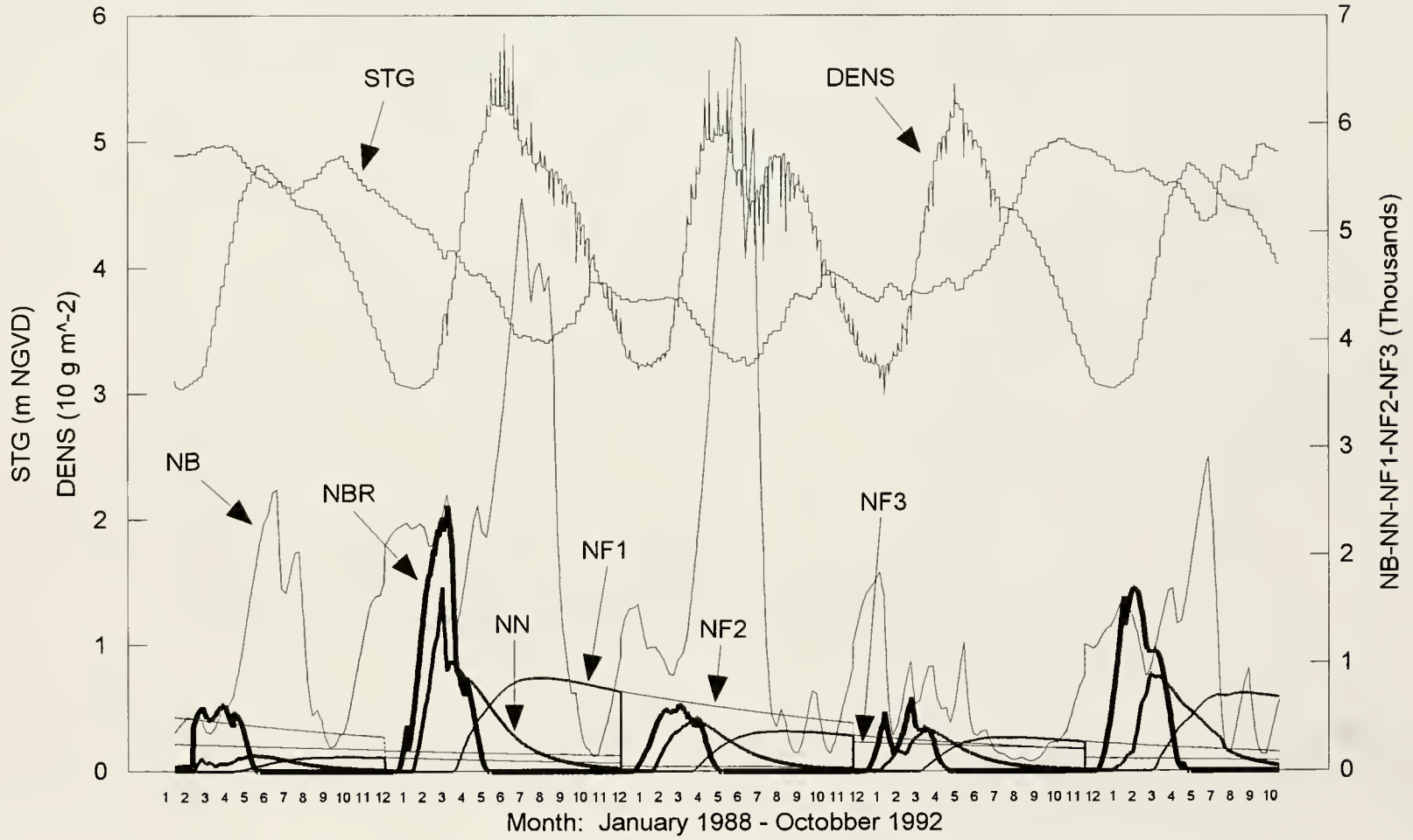

Figure 6-20. Standard simulation output of number of breeding Great Egrets (NBR), nestlings (NN), fledglings/first-year subadults (NF1), second year subadults (NF2), and third-year subadults (NF3) in relation to lake stage (STG), prey biomass density (DENS), and the number of foraging birds (NB).

significance of several climatic and hydrologic variables (Chapter 5). It is also consistent with their being a physiological-readiness restriction on nesting; i.e., breeding may not occur until photoperiod or other environmental cues trigger the redevelopment of sexual organs (Skutch 1976).

I explored other possibilities for reproducing the low nest counts in 1990 and 1991 relative to those in 1989 and 1992 (e.g., DENS and DR controls), but found that only a high-lake-stage attractor function produced the desired result. This suggested that nesting Great Egrets initiate nesting based on environmental cues that usually lead to peak food availability when nestlings are being fed, rather than on conditions being ideal at the time of egg-laying (as postulated by Lack 1954). In this case, high winter lake stages may typically ensure high prey productivity (Loftus et al 1990; Loftus and Eklund 1994), and in combination with the beginnings of a late-winter/spring surface-water recession (as occurred in 1989 and 1992) would normally guarantee high concentrations of prey in the near future.

This scenario is, however, contrary to recent evidence that Great Blue Herons begin nesting when prey intake is greatest, such that they often begin feeding young after the peak in prey availability has passed (Butler 1993). The reproductive effort of Great Blue Herons during my study followed the same pattern as for Great Egrets (Chapter 4), and the simulation results plot showing NBR in relation to prey density further suggested that nesting began when prey density was on the rise, rather than at peak levels (Fig. 6-20). The alternative hypothesis examined by Butler (1993) was formulated by Perrins (1965, 1970), and states that adults begin breeding after a threshold of prey availability and hence energy availability for egg production is passed. This was also the central assumption of Browder (1976) and directed her modeling effort for Wood Storks. However, Lack's and Perrin's hypotheses are not necessarily

mutually exclusive; i.e., breeding may not occur until an energy threshold for egg production is passed, but prey abundance still may increase beyond this threshold and reach a maximum when nestlings are being fed. In fact, in Butler's study, the peak in relative food availability occurred not at the time of egg-laying, but after chicks had hatched. However, prey availability declined before the nestlings' demand for food was greatest.

Butler (1993) argues that nesting adults may not be able to forecast future conditions because the peak in food availability at different locations varies too greatly. However, his study concerned birds that foraged in coastal lagoon habitats exposed by tidal flux. Local prey abundance may be difficult to predict over the long-term in marine habitats influenced daily by strong oceanic forces. In contrast, the annual wet-dry cycle characteristic of southern Florida (Deuver et al. 1994) is usually a relatively predictable phenomena, and wading birds that nest in the region are therefore probably more able to rely on forecasting future conditions to ensure an optimal allocation of their breeding effort. In fact, the reason for widespread declines in the success of Wood Stork nesting in Florida is in part that hydrologic manipulations have sufficiently reduced the consistency of the annual cycle that the storks are no longer able to reliably predict future conditions and now nest at inappropriate times (Ogden 1994). Similarly, during this study Great Egrets and Great Blue Herons initiated the lowest number of nests in 1990 (Fig. 6-1b), but both species achieved the highest per nest productivity in that year (Chapter 4). This also suggests that the birds were unable to reliably predict future conditions, in this case because the drought led to atypical conditions.

The only instance where the model failed to reproduce the observed trends in NBR was in 1988 (compare Figs. 6-1b and 6-20; 1988 data provided by the SFWMD). This was because the number of foraging birds (NB) attracted to the lake remained too

low during the time the seasonal control function allowed nesting to occur. The correct pattern arose only if I modeled breeder recruitment as a function of a maximum rate rather than as a function of NB. This suggested that birds sometimes breed at the lake even though foraging conditions on the lake are poor. Because the lake is surrounded by a dike that limits the outward expansion of the littoral zone, and to a lesser degree because lake water levels are regulated, hydrologic conditions inside and outside the dike often differ, particularly during high-water years. Specifically, the abrupt discontinuity created by the dike means that during high water years willow stands inside the dike still provide suitable nesting habitat, because birds can access suitable foraging habitat just outside the dike. In the absence of the dike, the rise in lake water levels would flood a much greater portion of the adjacent area, and birds would probably be forced to find other nesting areas nearer to habitats shallow enough for foraging. Thus, birds that use the lake for nesting and foraging are not necessarily responding to the same factors.

Reproductive Success and Productivity

As indicated above, the rate of prey consumption (J5) controlled hatching and fledging rates. Initially I modeled prey consumption as a linear function of minimum temperature (MINT), but found that an asymptotic, sigmoidal function was necessary to reproduce the observed patterns of annual variation in nest productivity. Specifically, my study of marked nests (Chapter 4) indicated that a cold snap in early 1989 caused many birds to abandon their nests, but the linear MINT function did not appear to allow a differential survival rate sufficient to reproduce the observed decline in hatching success. In other words, it appeared that the transition zone from acceptable temperatures to detrimental cold temperatures was narrow, and the negative effects of

cold temperatures increased exponentially once the threshold was crossed. Adult birds are probably versatile enough that they can employ alternative foraging strategies or simply persevere in the face of moderate drops in temperature, but prolonged or severe drops may quickly elicit widespread abandonment. However, part of the problem may have been that the input data were weekly averages rather than daily records, because this partially obscured the severity of shorter-term events. This may have been particularly true in 1991, because the simulations did not adequately account for a large-scale abandonment that occurred in early 1991 due in part to cold temperatures (Chapter 4). The only way I could get the model to respond with lower productivity in 1991 compared to 1990 was to force a high rate of egg loss (1.5 times the rate for other years). However, the opposite was true for 1992: with the MINT function adjusted to reproduce the trends observed in 1989, I had to force a reduced rate of egg loss (60% lower than in other years) to get 1992 productivity up to the observed levels. There were no severe cold snaps in 1992, but the average temperatures remained low throughout the month of January and into February. Additional fine-tuning of the MINT function may have accomplished a better balance, but it is likely that the model did not adequately account for some complex dynamics. Several sources of comparatively unpredictable egg and nestling mortality were not accounted for in the model; e.g., predation, disease, infertile eggs, congenital defects, accidents, parental incompetence, etc.

I also could not get the model to respond with higher productivity in 1990 compared to 1989 and 1991 unless I provided a mechanism for clutch to vary and added a supplemental food source. I was unable to discover a logical mechanism to get the model to yield a higher clutch size in 1990 without also producing a higher clutch size in 1989 (observed values: 2.7 in 1989, 3.1 in 1990, 2.8 in 1991, 2.9 in 1992;

1990 significantly higher than other years; Chapter 4). I therefore simply input different annual mean clutch sizes to study the effect. The real key to yielding higher productivity in 1990 than other years was, however, the addition of a supplemental food source. This provided further support for the contention that panhandling was an important supplementary food source for nesting Great Egrets in 1990. With the different annual mean clutch sizes, I obtained the expected increase in productivity by forcing an increased prey consumption rate of 1.12 times that allowed in other years. This corresponded remarkably well with the finding that panhandled fish constituted approximately 10% of the aggregate mass of food fed to nestlings in 1990 (McIvor and Smith 1992).

Without the above mentioned forced adjustments in clutch size, egg loss, and food supply, the model produced the second set of 1989-1992 annual productivity data shown in Table 6-1. The only instance where the output closely matched the observed results (the first set of data in Table 6-1) was for the percentage of hatched eggs that fledged. The third set of data shown in Table 6-1 gives the simulation results with the forced adjustments to egg loss and food supply incorporated. The match with the observed data is much better, but the input of different annual clutch sizes further improved the match for 1989 and 1990 per nest productivity (the last set of data in Table 6-1). Thus, without some artificial adjustments, the model did not perform particularly well in terms of productivity results. Adding a supplemental food source in 1990 matched field observations and therefore was reasonable. Allowing for fluctuations in clutch size also conformed with observations, and the addition of supplemental food in 1990 achieved the desired results for that year. However, I was unable to discover a logical mechanism to produce a lower mean clutch size in 1989. In addition, the adjustments to egg loss rates were entirely artificial, and indicated that

Table 6-1. Comparisons of observed nest production statistics (Chapter 4) and simulated responses with and without forced adjustments to annual mean clutch sizes, 1991 and 1992 egg survival rates, and the 1990 food supply.

Year	Number of Nests	% Eggs Hatched	% Hatched Eggs Fledged	% Eggs Fledged	Hatched Eggs Per Nest	Fledglings Per Nest
Observed Values						
1989	982[a]	55.2	48.9	27.0	1.4	0.7
1990	265[a]	66.2	62.4	40.8	2.0	1.2
1991	459[a]	42.5	57.1	24.1	1.2	0.7
1992	649[a]	59.2	36.0	21.3	1.6-1.8	0.6-1.2
No Clutch Control, No Forced Adjustments						
1989	1592	60.4	44.3	26.7	1.8	0.8
1990	386	61.7	55.3	34.1	1.8	1.0
1991	570	57.3	61.9	35.5	1.7	1.0
1992	1046	24.8	44.1	10.9	0.7	0.3
No Clutch Control, Forced Adjustments Added						
1989	464	60.4	44.3	26.7	1.8	0.8
1990	1592	66.6	60.7	40.4	1.9	1.2
1991	386	44.1	57.8	25.5	1.3	0.7
1992	570	55.0	54.8	30.1	1.6	0.9
Clutch Control, Forced Adjustments Added						
1989	1592	59.4	43.3	25.7	1.6	0.7
1990	386	67.3	61.1	41.1	2.1	1.3
1991	569	43.8	57.3	25.31	1.2	0.7
1992	1046	55.1	54.8	30.2	1.6	0.9

[a] Estimated peak number of nests, not necessarily the total number initiated.

the model did not adequately reflect the dynamics of nest-survival during the incubation phase. Probably what is needed are mechanisms to account for the variability of egg predation by crows, grackles and possibly snakes, and hydrologic and climatic data that more closely reflect conditions around individual nesting colonies. The age structure of the breeding population might also influence both mean clutch sizes and loss rates. The reproductive effort of Great Egrets was highest in 1989; perhaps more young birds nested during that year and laid smaller clutches than the average mature breeder. Unfortunately, obtaining age structure data for a large population of vagile birds is a difficult undertaking, and consequently there is very little data available on the subject.

Conclusion

I have herein summarized only the first step of the modeling process, that of building and quantifying a model that is logical and reproduces trends observed in the field over a period of time sufficient to reflect the dynamics of interest (Odum 1983). In fact, the first step is not yet complete, because additional work is needed to determine the mechanisms necessary to improve the model's performance with regards to annual levels of hatching success. In general, however, the next step in the process would be to validate the model by testing its performance to see if it reproduced trends observed under differing sets of environmental conditions. Additional data is available concerning general population trends at the lake for the twelve-year period prior to the study (David 1994a, b), but no additional information is available concerning reproductive success. Therefore, a rigorous validation was not possible and I did not proceed further. Nonetheless, the model-building effort did help to confirm some of the principal relationships summarized in other chapters, and highlighted areas where additional work and knowledge is needed.

To summarize, the modeling exercise provided additional support for the following conclusions:

1) Actual prey density was higher at the peak of the drought than the model predicted when prey production was modeled as a linear function of surface water area. This fact suggested that prey species were able to maintain relatively high fecundity after migrating and concentrating in a restricted area of submerged vegetation habitats.

2) Although general increases in foraging bird numbers in 1989 and 1990 were probably responses to large-scale surface-water recessions that concentrated prey, the extreme peaks in abundance and the increase in species diversity at the height of the drought periods most likely reflected a regional drought-refuge response.

3) The dominant importance of the drying-rate functions as the mechanism of immigration and emigration control suggested that water area and water depth alone do not adequately account for wading bird foraging population responses. Instead, it is more likely that the pattern and rate of surface-water change and localized patterns of prey concentration are the keys to understanding the population responses.

4) The need for a seasonal control on breeding in the model, suggested that hydrologic and climatic forces are proximate rather than ultimate cues for breeding.

5) A high late-winter stage attractor was necessary to reproduce the observed trends in Great Egret reproductive effort, confirming that a high winter stage followed by an early spring surface-water recession is the combination that most attracts Great Egrets for nesting at the lake.

6) The model did not adequately reproduce the level of reproductive effort observed in 1988. This provided support for the contention that birds may choose to nest on the lake even though foraging conditions within the diked boundaries of the lake are poor.

7) With regards to the negative influence of declining temperatures on foraging efficiency and therefore nest productivity, the simulation results suggested that there is an abrupt-threshold response, rather than a linear association between foraging efficiency and minimum temperatures.

8) The model did not adequately reproduce the observed trends in egg production and hatching success, suggesting that the causes of abandonment and failure during incubation were complex and probably more localized in nature than the lakewide hydrologic and climatic data represented.

9) Adding a supplemental food source during 1990--panhandled fish--accounted for a discrepancy between the simulated and observed productivity statistics. The amount of extra food required closely matched the estimated contribution to nestling diets. These findings supported the hypothesis that panhandling was an effective alternative foraging strategy for Great Egrets during the drought.

CHAPTER 7
PROJECT SUMMARY

To summarize the results and conclusions derived from the previous chapters, I present the following outline.

Species Studied

A. Foraging Distribution and Abundance (Chapter 2)

   Great Blue Heron, Great Egret, Snowy Egret, Tricolored Heron, Little Blue Heron, White Ibis, Glossy Ibis, Wood Stork, Roseate Spoonbill, (Great White Heron)

B. Foraging Habitat Selection (Chapter 2)

   Great Blue Heron, Great Egret, Snowy Egret, Tricolored Heron, Little Blue Heron, White Ibis

C. Nesting Adult Foraging Flights and Habitat Selection (Chapter 3)

   Great Egret, Snowy Egret, Tricolored Heron, White Ibis

D. Nesting Activity and Nest Success Studies (Chapters 4 and 5)

   Great Blue Heron, Great Egret, Snowy Egret, Tricolored Heron, Little Blue Heron, White Ibis

E. Population Model (Chapter 6)

   Great Egret

Results and Observations

A. The Abundance of Foraging Birds (Chapter 2)

1. The highest numbers and diversity of foraging birds gathered on the lake in 1989 and especially 1990 during peak drought periods when large-scale surface-water recessions occurred:

   a) Prey sampling by Chick and McIvor (1994) and the author demonstrated that forage fishes and grass shrimp were heavily concentrated in thick, exposed beds of Hydrilla and Vallisneria.

⇒ concentrated prey resulting from surface-water recessions a strong attractor for foraging birds

2. Uncommon Wood Storks and Roseate Spoonbills were prevalent on the lake only during drought periods:

   a) Moderate numbers of storks fed in receding upper-elevation pools in Nymphaea-dominated wet prairie habitats early in 1989; otherwise, large flocks were observed only in submerged vegetation habitats in Fisheating Bay at the height of the 1989 and especially 1990 drought periods.

   b) An unusual concentration of 75-125 immature spoonbills remained at the lake for 10-12 weeks in 1990 during the drought.

⇒ evidence for regional drought refuge response

3. High lake stages (>4.5 m NGVD) precluded access to most habitats on the lake and led to low foraging populations; low lake stages (<3.7 m NGVD) also greatly reduced the area available for foraging, but resulted in highly concentrated prey

that attracted many birds; the lack of a spring surface-water recession in 1991 resulted in the lowest numbers of foraging birds, despite moderate stages.

⇒ lake stage determines the extent of habitat available; otherwise, the pattern of surface-water fluctuation is the primary determinant of population levels on the lake

B. Habitat Selection Among the General Foraging Population (Chapter 2)

1. During peak drought periods with low lake stages, large numbers of all species were attracted to exposed beds of submerged vegetation, but species differed in their tendency to select such habitats:

   a) Snowy Egrets showed strong selection for primarily Hydrilla-dominated habitats regardless of the lake stage;

      i. used aerial foraging techniques over deep-water areas.

      ii. used topped mats of Hydrilla, floating Eichhornia, and surface leaves of Nelumbo for support and for aerial-foraging launch platforms

   b) A few Great Egrets foraged over deep Hydrilla and Potamogeton beds in 1991 using aerial techniques;

      i. persistent winds facilitated activity.

      ii. diet of nestlings fed by adults using technique included an unusual variety of larger fishes including sunfish, immature gar, and golden shiners, and nest productivity was high.

   c) White Ibises appeared to switch from an invertebrate-dominated diet to foraging on concentrated fish around beds of submerged vegetation only during peak drought periods at the lowest lake stages.

d) Tricolored Herons regularly used the surface leaves of Nelumbo for support in prey-rich Hydrilla beds too deep for wading; otherwise, Tricolored and Little Blue herons showed the weakest overall selection for submerged habitats.

2. Open, lakeward-fringe habitats were always underutilized relative to their availability, but several species used such habitats at the lowest lake stages;
   a) At very low lake stages (<3.3 m NGVD), Great Blue Herons, Great Egrets and Wood Storks frequently congregated in large numbers (10's to 100's) in open water to feed on concentrated schooling fish and nesting sunfish.
   b) Similarly, mixed groups of 20-30 Snowy Egrets and Tricolored Herons occasionally collected in shallow open water areas and chased schooling fish.
3. Great Blue and Great White Herons were unique in that many individuals foraged from rocks and by wading out from open-water "beaches" along the eastern margin.
4. Relatively few birds foraged on the lake at high stages, but mixed-grass and Rhynchospora-dominated upper-elevation habitats drew what concentrated flocks there were:
   a) Great Egrets were particularly attracted to mixed-grass habitats on Indian Prairie;
      i. drought-related fires cleared thick Panicum wrack and upon reflooding produced more open stands that were the focus of Great Egret foraging in 1992.
   b) Little Blue Herons and White Ibises were particularly attracted to western-margin Rhynchospora flats;

i. the encroachment of Melaleuca into these habitat areas was one of the few negative results of the drought.

5. Except at the lowest and highest lake stages, emergent wet-prairie habitats featuring Eleocharis, with Panicum, Nymphaea, and sparse Typha common additions, were the most consistently selected habitats:
   a) Strongest selection among Great Egrets, Tricolored Herons, and Little Blue Herons.
6. Mixed-successional habitat complexes flourished following periods of drought, fire and reflooding, and by virtue of their abundance attracted many foraging birds; however, selection was often neutral rather than positive:
   a) Areas featuring diverse, mixed-stature assemblages were the primary attractors.
   b) White and especially Glossy Ibises, and Snowy Egrets and Tricolored Herons showed the strongest selection for complex successional habitats.
   c) Patches of Polygonum were a focus of Great Egret foraging.
   d) Areas of decaying vegetation attracted ibises.
7. Thick stands of Typha and Cladium rarely attracted foraging birds:
   a) Drought-related fires cleared thick Typha wrack and upon reflooding produced more open stands of Typha where other emergents such as Polygonum and Nymphaea emerged--these habitat mixes attracted foraging birds.
8. Heavily wooded--Salix and Melaleuca--habitat patches rarely attracted foraging birds, but Salix was the primary nesting substrate.

⇒ patterns (d) - (f) emphasized the importance of emergent vegetation mixes of moderate stature and structural complexity.

C. Foraging-Flight Dynamics and Nest Productivity (Chapter 3)

1. There was little evidence to suggest that variation in the distances traveled by nesting adults to foraging grounds significantly affected levels of nest success and productivity among the four species studied.
    a) The possible exception was Tricolored Herons--flight distances were significantly and negatively correlated with colony-specific estimates of nest success and nestling production, but the data were limited in scope.

D. Patterns of Foraging Habitat Use Among Nesting Adults (Chapter 3)

1. Habitat selection among nesting adults reflected tendencies similar to those demonstrated for the general foraging population, but placed more emphasis on use of off-lake habitats;
    a) Further emphasized the tendency of Great Egrets and White Ibises to focus on foraging in mixed wet-prairie habitats at all but the lowest stages.
    b) Further emphasized the tendency of Snowy Egrets to focus on foraging in deep-water Hydrilla habitats using aerial techniques and Eichhornia, Nelumbo leaves, and topped mats of Hydrilla for support.
2. Species nesting on the lake differed in their tendency to use off-lake habitats for foraging:
    a) Throughout the study, regardless of hydrologic conditions, significant proportions (>20%) of the Great Egrets and White Ibises that nested on the lake foraged in adjacent off-lake habitats;
    b) White Ibises most at high lake stages, but also more at low as opposed to moderate lake stages--favored flooded pastures, pasture ditches, isolated pasture wetlands, shallow sloughs, and cattle feedlots.

c) Great Egrets slightly more at higher as opposed to moderate lake stages, but most at low lake stages--primarily pasture wetlands at high lake stages, primarily panhandling to the north and sugar cane field ditches to the south at low lake stages.

d) Snowy Egrets regularly turned to off-lake habitats only at high lake stages--primarily sugar-cane field ditches near Clewiston.

e) Documentation was poorest for Tricolored Herons, but it appeared that birds nesting on-lake tended to forage on-lake.

3. Great Egrets were particularly unique because they resorted to panhandling at residential fish-cleaning stations and stealing bait minnows from bait shop tanks, particularly during the drought in 1990.

E. Foraging Sociability of Nesting Adults (Chapter 3)

1. White Ibises were the most social of the species studied:

a) More inclined to depart in groups than alone, and traveled in larger groups than other species.

b) Rarely landed in areas devoid of other foraging birds and usually landed in the immediate vicinity of others as opposed to just nearby.

c) Tended to join larger flocks than other species.

d) Usually joined flocks containing conspecifics, but frequently joined flocks including Snowy Egrets.

⇒ Consistent with evidence that the species' unique grope foraging technique renders habitat selection strategies the primary determinant of foraging efficiency, and flocking and group foraging help insure the selection of profitable foraging habitat.

2. Snowy Egrets ranked second highest in terms of sociability:
    a) More likely to travel in groups and land with traveling companions than Great Egrets and Tricolored Herons, but more likely to travel alone than in groups.
    b) Traveled in smaller groups than White Ibises.
    c) More likely than Great Egrets and Tricolored Herons to join other birds at feeding sites, and usually landed in the immediate vicinity of others.
    d) Tended to join smaller flocks than White Ibises.
    e) Usually joined flocks that included conspecifics.
3. Great Egrets ranked second lowest in terms of sociability:
    a) Least likely to depart in groups, but more likely than Tricolored Herons to land with traveling companions.
    b) Traveled in smaller groups than White Ibises.
    c) More likely than Snowy Egrets and White Ibises to land in areas devoid of other birds, and conversely less likely to land in the immediate vicinity of other birds.
    d) Tended to land with smaller groups than White Ibises, but with larger groups than Tricolored Herons.
    e) Both the presence of conspecifics and the presence of Snowy Egrets appeared to act as attractors.

⇒ Tendency toward solitary foraging consistent with species frequent use of slow-stalking foraging strategy and tendency to focus on somewhat larger prey in deeper habitats.

4. Tricolored Herons were the least social of the four species studied:
    a) Departed colonies in groups more often than Great Egrets, but rarely landed with traveling companions.
    b) Traveled in smaller groups than White Ibises.
    c) Least likely to join other birds on foraging grounds; overall more likely to land alone or only near other birds as opposed to in the immediate vicinity of others; and joined smaller groups than other species.
    d) Presence of conspecifics did not appear to influence choice of landing spots, whereas the presence of Snowy Egrets appeared to act as an attractor.

⇒ Tendency toward solitary foraging consistent with species frequent use of active disturb-and-chase foraging strategy and use of cryptic coloration to forage at the edges of vegetation along canals and adjacent to open habitats.

F. Colony Locations and Interannual Turnover (Chapter 4)

1. During the peak drought year of 1990 and subsequently in 1991 before the lake stage returned to high levels, nesting activity shifted from interior-marsh sites to almost exclusively small spoil islands and other islands still surrounded by water--both on and off the lake--and nest success and productivity were generally high.

2. The largest number and variety of colony sites was used during 1992 when the lake stage remained high throughout the nesting season, but for most species this did not translate to higher nest success:
    a) Great Blue Herons were the primary exception, although success was not higher than in 1990.

b) High and fluctuating water levels appeared to contribute to several colony abandonments among particularly the small herons.

⇒ Moderate lake stages provide a variety of colony sites as well as a diverse array of accessible foraging habitats.

G. Reproductive Effort and Hydrologic Trends (Chapter 4)

1. The largest two species, Great Blue Herons and Great Egrets, initiated the most nests in 1989 and 1992 following high winter stages and the early onset of a steady spring surface-water recession.

2. Little Blue Herons initiated the most nests in 1989, following three years of high lake stages and the onset of a large-scale surface-water recession:

   a) The lack of a similar response in 1992 suggested that the antecedent high-water period was the key to understanding the trend;

      i. the extended period of high water probably led to dense and widespread populations of a favored prey species, grass shrimp--the recession then concentrated the shrimp and led to high foraging success.

3. Snowy Egrets and Tricolored Herons initiated the most nests during the peak drought year of 1990, and the least during the highest-water year of 1992.

4. White Ibis nesting was particularly synchronized with periods of receding water--including unusually late waves of nesting--less so with lake stage per se; nest numbers were lowest in 1991 when no large-scale recession occurred.

⇒ Suggests that the best scenario for nesting is consistently high fall/winter stages followed by early, protracted, and steady spring recessions that bring the lake stage down to at least moderate levels.

H. Annual Nest Success and Nestling Production (Chapter 4)

1. Both Great Egrets and Great Blue Herons initiated more nests in 1989, but achieved higher nest success and per nest productivity in 1990.

2. Little Blue Herons initiated more nests and achieved the highest per nest productivity in 1989, with 1990 ranking second best.

3. White Ibis nest success and productivity was highest in 1989, but not much higher than in 1990.

4. Annual variation in Snowy Egret and Tricolored Heron nest success and productivity generally followed the same pattern shown for nest numbers, but annual variation was less pronounced than for other species.

⇒ All species profited from the concentrated prey resources produced by the drought, but Great Egrets also augmented the supply of food they provided their nestlings in 1990 with panhandled fish scraps

I. Colony Success and Foraging Habitat Types (Chapters 3, 4)

1. Except for episodes of alligator predation, all nesting species fared well at the interior-marsh Moore Haven colony in 1989--water levels were dropping steadily after three years of high water and foraging was focused in mixed wet-prairie habitats.

2. Snowy Egrets, and Tricolored Herons that nested on spoil islands in Fisheating Bay in 1990 and 1991--and Great Egrets in 1991--fed within primarily thick beds of submerged vegetation and generally fared very well:
    a) Thick topped-mats of Hydrilla, intermixed Nelumbo, and floating mats of Eichhornia all proliferated in the wake of the drought; Snowy Egrets and Tricolored Herons, in particular, took advantage of these vegetation types for support in deep water, and their high nest success in 1991 compared to other species probably reflected this tendency and the fact that the strategy rendered them less dependent on on-lake hydrology to produce favorable foraging conditions.

3. In 1990, nestling Great Egrets were parasitized by the nematode Eustrongylides ignotus more often at Clewiston Spit than at Eagle Bay Island. Clewiston adults foraged primarily in sugar-cane field ditches, whereas Eagle Bay Island adults foraged in submerged beds and off-lake pasture-pocket and slough wetlands, and panhandled fish scraps:
    a) Samples of forage fishes collected on the lake revealed very few infected individuals, suggesting that most of the parasitic infections of birds came from off-lake habitats.

⇒ A critical need for additional study.

J. Determinants of Nest Failure (Chapters 4, 5)

1. Mean lake stage:
    a) A decrease in the mean lake stage generally decreased the probability of nest failure--except at the height of the drought--but as a determinant of

nest failure, mean water level usually ranked low in importance compared to water level trends.

2. Surface-water dynamics:
    a) For most species, nest survival increased substantially during rapid and particularly steady and protracted surface-water recessions.
    b) However, for most species, the probability of nest failure also declined during periods of slowly but steadily rising water, especially at higher lake stages;
        i. Snowy Egrets an exception.
        ii. strongest relationship for Great Egrets and White Ibises.
3. Rainfall:
    a) High short-term rainfall increased the probability of failure if it contributed to abrupt or large-scale reversals in established drying trends.
    b) However, consistent rainfall over the long-term probably allowed isolated ephemeral wetlands and the associated prey populations to persist during drought periods, and thereby increased the probability of nest survival.
    c) The combination of cold and rainy weather increased the probability of nest failure.

⇒ Mean water levels were a determinant of reproductive effort more than of nest success; nest success was highest when water levels were receding steadily, but most species also benefited from slowly rising water at high stages; consistent rainfall improved the chance of success during the drought.

4. Date of nest initiation:
    a) A strong determinant of nest failure in all species' models--as long as early-season losses due to cold weather were accounted for by the minimum temperature variable--with the probability of failure always increasing as the season progressed;
        i. hypothesis -- mature and successful breeders tend to nest first and therefore the probability of success declines later in the season as less experienced breeders attempt to nest.
        ii. another possibility -- individual hydrologic and climatic factors do not adequately reflect the combined, seasonally-integrated effects of many environmental factors.
5. Cold temperatures:
    a) Decreasing temperatures usually increased the probability of nest failure among all species, but increasing temperatures became a liability during peak drought periods; i.e., at low lake stages following prolonged drying and when rainfall remained scarce;
        i. strongest cold effects shown for early-nesting Great Blue Herons and Great Egrets.
6. Wind:
    a) Strong winds led to the failure of 10% of the Great Blue Heron nests by dislodging nests, eggs, and nestlings and snapping the tops of the tall willow branches that the species often chose for nesting;
        i. manifested as a significant positive association between nest height and the probability of failure.

7. Predation:
    a) Generally an uncommon source of failure, but: crows and grackles preyed upon eggs; Black-crowned Night Herons preyed upon small nestlings; raptors occasionally preyed upon nestlings and at least one adult Snowy Egret; Rat Snakes and Eastern Cottonmouths may have taken some eggs and/or nestlings; and alligators preyed upon nestlings and destroyed several nests at the Moore Haven colony.
        i. variation in nest height and overhead cover probably influenced predation rates among the small herons.
8. Disease and parasites:
    a) Eustrongylidosis can be a significant threat to nestling survival; infections significantly reduced the growth and survival of Great Egret nestlings in 1990.
        i. parasitism may increase if artificially nutrient-enriched and disturbed habitats proliferate.
    b) Besides deaths due to eustrongylidosis, necropsy exams of nestlings revealed causes of death including a congenital heart defect, malaria, liver, lung, intestinal and kidney disease, metabolic bone disease, pneumonia, and bacterial and viral infections.
    c) Although disease and parasitism claimed the lives of many nestlings, disease could rarely be assigned as the reason for a whole-nest failure.

⇒ Unmanageable stochastic disturbances, intrinsic biological characteristics, predation, and disease may be responsible for significant proportions of nest failures, but the negative impacts of such factors will be mediated by habitat and water-level

management strategies that insure otherwise favorable nesting and foraging conditions for wading birds.

Conclusions and Management Recommendations

A. Hydrologic trends determine the availability and profitability of foraging habitat and influence the timing, location, intensity, and success of nesting efforts. Lake regulation schedules and water level management are therefore primary concerns for wading bird management.

B. Different species respond to hydrologic variation in unique ways, but all species should prosper if the average year includes relatively high fall/winter water levels followed by a steady spring surface-water recession that begins around January, lasts for 4-5 months, and brings the lake stage down to moderate levels.

C. Excessively high lake stages eliminate foraging and nesting habitat, but higher lake levels would be less of a problem if the littoral zone could expand—as it did historically—further up Indian Prairie and along the Kissimmee River or in a wider front up Fisheating Creek and along Nicodemus Slough, or if more of the pocket and slough wetlands to the north and west of the lake were managed to support waterbirds.

D. Conditions at Lake Okeechobee need not be ideal for nesting and foraging every year, because wading birds are gregarious and capable of ranging throughout southern Florida in search of suitable habitat. However, a high level of regional management planning is necessary to guarantee that sufficient high-quality habitat always is available somewhere in the region.

E. Overall, results from my study and from a variety of studies in the Everglades emphasize that the best management strategy should incorporate the flexibility to allow hydrologic conditions to fluctuate naturally. Management for wide expanses of diverse, long-hydroperiod, moderate-depth marshland should be the focus, but wading birds may benefit in the long run from intermittent periods of high water and periodic large-scale recessions if they can access alternate nesting and foraging sites in the short run.

F. Lake Okeechobee is a very large lake, and during a severe drought retains water when most of the surrounding marshland and the Everglades are dry. Record numbers of birds, including unusually large numbers of typically uncommon Wood Storks and rare Roseate Spoonbills congregated on the lake during the 1989/90 drought. This suggests that Lake Okeechobee and other large lacustrine systems with fringing marshland serve as important drought refuges for both aquatic prey organisms and vagile predators such as wading birds.

APPENDIX A
FORAGING WADING BIRD POPULATION ESTIMATES BY SPECIES AND SURVEY

Survey Date	Great Blue Heron Transects	std. err.	East-South Route	Eagle Bay Island	Total	Great White Heron East South Route	Eagle Bay Island	Total
08-Aug-88	8	-	-	-	8	-	-	-
17-Sep-88	12	-	17	4	33	0	0	0
16-Oct-88	43	-	66	4	113	0	0	0
19-Nov-88	109	-	61	5	175	0	0	0
17-Dec-88	201	-	90	18	309	0	0	0
14-Jan-89	310	-	83	19	412	0	0	0
30-Jan-89	267	31.0	76	1	344	0	0	0
11-Feb-89	517	143.2	93	9	619	0	0	0
28-Feb-89	640	242.9	87	8	735	0	0	0
15-Mar-89	567	154.8	102	14	683	0	0	0
27-Mar-89	830	495.9	80	10	920	0	0	0
10-Apr-89	500	140.2	70	22	592	0	0	0
25-Apr-89	273	45.6	33	18	324	0	0	0
09-May-89	327	47.0	62	31	420	2	0	2
22-May-89	580	134.9	74	28	682	0	0	0
07-Jun-89	1290	498.2	81	16	1387	0	0	0
19-Jun-89	2180	934.4	145	8	2333	0	0	0
05-Jul-89	550	96.2	105	11	666	0	0	0
23-Jul-89	240	47.0	55	11	306	1	0	1
08-Aug-89	400	88.0	135	18	553	0	0	0
25-Jan-90	250	34.2	97	14	361	0	0	0
09-Feb-90	270	41.6	145	25	440	0	0	0
22-Feb-90	190	27.4	61	10	261	0	0	0
09-Mar-90	217	26.3	92	9	318	0	0	0
24-Mar-90	363	62.9	143	21	527	0	0	0
07-Apr-90	607	133.8	136	16	759	3	0	3
20-Apr-90	233	49.6	168	8	409	3	0	3
05-May-90	340	74.7	146	61	547	1	0	1
18-May-90	430	106.8	171	75	676	2	0	2
01-Jun-90	980	308.3	231	51	1262	1	0	1
14-Jun-90	713	178.4	156	26	895	2	0	2
28-Jun-90	637	204.3	158	41	836	3	0	3
13-Jul-90	200	49.4	108	35	343	4	0	4
25-Jul-90	133	24.7	107	65	305	4	0	4
09-Aug-90	147	26.4	46	14	207	4	0	4
14-Jan-91	-	-	76	10	-	0	0	0
04-Feb-91	-	-	65	12	-	1	0	1
19-Feb-91	-	-	70	11	-	0	0	0
05-Mar-91	-	-	70	19	-	1	0	1
19-Mar-91	-	-	54	19	-	0	0	0
30-Mar-91	278	-	91	5	374	0	0	0
13-Apr-91	133	23.9	57	21	211	0	1	1
27-Apr-91	97	19.7	43	5	145	3	0	3
10-May-91	110	26.1	38	5	153	0	0	0
25-May-91	107	18.2	17	4	128	0	0	0
08-Jun-91	57	11.9	27	6	90	0	0	0
22-Jun-91	43	18.5	37	2	82	7	0	7
09-Jul-91	53	14.2	16	4	73	1	0	1
22-Jul-91	50	10.9	6	3	59	0	0	0
04-Aug-91	23	8.1	17	3	43	0	0	0
01-Sep-91	33	10.2	11	6	50	0	0	0
18-Jan-92	157	25.5	98	10	265	0	0	0
18-Feb-92	177	26.0	151	11	339	0	0	0
12-Mar-92	133	39.4	102	14	249	0	0	0
16-Apr-92	67	14.1	18	9	94	0	0	0
22-May-92	43	10.1	34	4	81	0	0	0
19-Jun-92	73	12.3	35	3	111	2	0	2
18-Jul-92	86	26.6	22	0	108	0	0	0
15-Aug-92	10	4.6	20	4	34	0	0	0

Great Egret

Survey Date	Transects	std. err.	East-South Route	Eagle Bay Island	Total
08-Aug-88	652	-	-	-	652
17-Sep-88	1336	-	21	4	1361
16-Oct-88	1419	-	65	10	1494
19-Nov-88	1486	-	48	9	1543
17-Dec-88	1329	-	67	19	1415
14-Jan-89	1916	-	50	52	2018
30-Jan-89	1453	189.3	78	4	1535
11-Feb-89	1817	301.3	121	45	1983
28-Feb-89	2940	533.9	299	23	3262
15-Mar-89	2673	549.7	159	7	2839
27-Mar-89	2330	517.4	130	13	2473
10-Apr-89	3860	913.7	130	5	3995
25-Apr-89	1833	365.3	93	7	1933
09-May-89	2273	415.1	168	21	2462
22-May-89	5623	1639.9	196	34	5853
07-Jun-89	5190	1374.4	344	11	5545
19-Jun-89	8080	2438.8	477	6	8563
05-Jul-89	3117	572.2	212	15	3344
23-Jul-89	2387	482.4	577	33	2997
08-Aug-89	3053	738.1	518	42	3613
25-Jan-90	610	101.3	143	16	769
09-Feb-90	930	158.2	169	51	1150
22-Feb-90	893	130.9	168	14	1075
09-Mar-90	757	113.3	106	29	892
24-Mar-90	1343	270.8	121	18	1482
07-Apr-90	2297	487.2	222	34	2553
20-Apr-90	1003	191.8	359	16	1378
05-May-90	2427	605.7	472	70	2969
18-May-90	2847	814.6	452	117	3416
01-Jun-90	4013	1310.3	286	172	4471
14-Jun-90	9960	4189.3	793	165	10918
28-Jun-90	2570	519.3	1036	199	3805
13-Jul-90	1640	403.3	316	166	2122
25-Jul-90	753	159.1	191	100	1044
09-Aug-90	593	115.4	149	66	808
14-Jan-91	-	-	96	66	-
04-Feb-91	-	-	90	38	-
19-Feb-91	-	-	88	21	-
05-Mar-91	-	-	130	29	-
19-Mar-91	-	-	85	29	-
30-Mar-91	801	-	84	49	934
13-Apr-91	607	100.7	51	6	664
27-Apr-91	680	102.6	65	13	758
10-May-91	417	63.7	81	15	513
25-May-91	583	66.7	62	29	674
08-Jun-91	597	91.8	86	28	711
22-Jun-91	320	54.0	68	35	423
09-Jul-91	303	49.9	102	30	435
22-Jul-91	323	41.5	71	21	415
04-Aug-91	300	51.4	86	22	408
01-Sep-91	627	77.9	84	7	718
18-Jan-92	1373	196.1	175	13	1561
18-Feb-92	1467	132.1	154	17	1638
12-Mar-92	1310	389.3	157	8	1475
16-Apr-92	1657	176.1	125	16	1798
22-May-92	1427	142.4	125	37	1589
19-Jun-92	2053	215.9	116	36	2205
18-Jul-92	258	51.0	22	1	281
15-Aug-92	1203	177.7	43	28	1274

Snowy Egret

Survey Date	Transects	std. err.	East-South Route	Eagle Bay Island	Total
08-Aug-88	4	-	-	-	4
17-Sep-88	32	-	4	5	41
16-Oct-88	31	-	5	1	37
19-Nov-88	52	-	11	0	63
17-Dec-88	33	-	2	4	39
14-Jan-89	8	-	6	17	31
30-Jan-89	67	27.9	13	0	80
11-Feb-89	7	3.9	7	0	14
28-Feb-89	100	40.9	0	0	100
15-Mar-89	57	19.7	55	0	112
27-Mar-89	17	5.8	11	0	28
10-Apr-89	87	26.5	3	1	91
25-Apr-89	83	15.4	1	2	86
09-May-89	150	27.3	5	0	155
22-May-89	113	24.7	4	0	117
07-Jun-89	103	26.1	14	4	121
19-Jun-89	897	699.4	170	9	1076
05-Jul-89	210	92.2	21	2	233
23-Jul-89	63	24.5	44	0	107
08-Aug-89	20	8.2	92	0	112
25-Jan-90	23	11.8	21	3	47
09-Feb-90	7	3.9	28	0	35
22-Feb-90	60	27.3	80	9	149
09-Mar-90	10	4.6	24	0	34
24-Mar-90	33	15.5	14	0	47
07-Apr-90	67	19.3	20	0	87
20-Apr-90	90	22.8	40	24	154
05-May-90	100	26.9	61	2	163
18-May-90	40	12.6	45	0	85
01-Jun-90	187	84.6	31	2	220
14-Jun-90	227	78.4	26	52	305
28-Jun-90	147	35.3	147	2	296
13-Jul-90	107	42.3	25	4	136
25-Jul-90	70	27.2	0	0	70
09-Aug-90	73	50.3	0	1	74
14-Jan-91	-	-	9	1	-
04-Feb-91	-	-	39	26	-
19-Feb-91	-	-	39	3	-
05-Mar-91	-	-	2	4	-
19-Mar-91	-	-	0	1	-
30-Mar-91	324	-	4	1	329
13-Apr-91	77	22.9	0	2	79
27-Apr-91	147	63.3	16	6	169
10-May-91	117	48.0	19	3	139
25-May-91	193	88.0	13	62	268
08-Jun-91	143	56.8	33	91	267
22-Jun-91	40	18.5	9	26	75
09-Jul-91	43	17.9	4	18	65
22-Jul-91	60	18.1	6	28	94
04-Aug-91	37	12.9	10	34	81
01-Sep-91	143	45.6	10	22	175
18-Jan-92	7	4.0	1	11	19
18-Feb-92	70	28.1	13	1	84
12-Mar-92	47	19.3	8	0	55
16-Apr-92	53	14.9	11	16	80
22-May-92	40	14.8	6	46	92
19-Jun-92	87	26.5	34	27	148
18-Jul-92	73	48.4	3	8	84
15-Aug-92	100	40.7	10	22	132

Unidentified Small White Ardeid

Transects	std. err.	East-South Route	Eagle Bay Island	Total	SWA Total
426	-	-	-	426	430
800	-	17	6	823	864
1013	-	23	9	1045	1082
704	-	16	7	727	790
955	-	2	11	968	1007
928	-	40	244	1212	1243
1203	279.3	141	0	1344	1424
913	288.5	84	210	1207	1221
1417	321.6	290	0	1707	1807
2003	480.5	191	5	2199	2311
2010	404.8	65	35	2110	2138
4363	561.1	58	2	4423	4514
950	231.3	22	2	974	1060
913	190.6	93	12	1018	1173
2210	603.7	174	9	2393	2510
2113	468.0	322	15	2450	2571
4204	885.5	266	31	4501	5577
3567	818.7	203	29	3799	4032
1573	566.6	205	27	1805	1912
2780	992.4	155	34	2969	3081
583	123.6	184	8	775	822
957	232.4	123	1	1081	1116
457	118.8	234	36	727	876
1067	385.9	99	13	1179	1213
1220	262.5	82	7	1309	1356
1180	262.5	221	79	1480	1567
1277	326.0	276	36	1589	1743
1353	329.3	310	33	1696	1859
1930	497.4	423	0	2353	2438
3147	646.4	504	23	3674	3894
5427	1661.1	540	117	6084	6389
1557	283.0	526	207	2290	2586
2727	620.2	308	50	3085	3221
1727	667.0	23	44	1794	1864
1433	480.3	7	19	1459	1533
-	-	35	52	-	-
-	-	296	56	-	-
-	-	64	65	-	-
-	-	52	121	-	-
-	-	28	24	-	-
298	-	123	36	457	786
347	110.8	20	12	379	458
250	85.0	12	15	277	446
217	115.5	14	24	255	394
733	548.5	0	21	754	1022
227	59.3	7	6	240	507
220	128.3	6	24	250	325
290	84.3	79	48	417	482
347	91.3	134	88	569	663
417	74.8	385	115	917	998
1023	182.4	286	85	1394	1569
2417	367.1	666	90	3173	3192
1790	231.0	874	87	2751	2835
2837	626.5	561	83	3481	3536
1280	163.6	167	39	1486	1566
590	96.1	148	17	755	847
1130	463.4	285	66	1481	1629
86	47.7	18	1	105	189
1050	301.4	23	56	1129	1261

Survey Date	Tricolored Heron					Little Blue Heron				
	Transects	std. err.	East South Route	Eagle Bay Island	Total	Transects	std. err.	East South Route	Eagle Bay Island	Total
08-Aug-88	6	-	-	-	6	16	-	-	-	16
17-Sep-88	0	-	0	4	4	72	-	6	0	78
16-Oct-88	3	-	1	0	4	34	-	8	1	43
19-Nov-88	6	-	2	4	12	32	-	6	1	39
17-Dec-88	23	-	5	2	30	124	-	2	0	126
14-Jan-89	28	-	8	0	36	186	-	26	2	214
30-Jan-89	47	13.3	2	0	49	233	75.7	6	0	239
11-Feb-89	27	12.5	8	3	38	57	28.9	21	0	78
28-Feb-89	13	5.4	5	2	20	240	111.6	11	0	251
15-Mar-89	47	11.1	5	0	52	500	158.4	54	0	554
27-Mar-89	27	7.0	13	0	40	20	7.4	4	1	25
10-Apr-89	50	16.5	5	5	60	57	15.7	5	1	63
25-Apr-89	20	6.4	11	3	34	7	3.9	4	0	11
09-May-89	30	7.3	9	3	42	23	6.6	3	0	26
22-May-89	147	70.9	10	1	158	193	112.5	12	0	205
07-Jun-89	37	10.7	18	5	60	163	86.4	56	2	221
19-Jun-89	83	20.4	50	6	139	833	371.4	142	2	977
05-Jul-89	90	20.6	41	13	144	257	57.4	65	0	322
23-Jul-89	100	24.5	36	6	142	287	88.4	22	1	310
08-Aug-89	83	24.9	26	4	113	150	26.9	45	0	195
25-Jan-90	17	6.0	11	1	29	60	18.5	10	5	75
09-Feb-90	27	9.0	7	0	34	110	49.9	22	8	140
22-Feb-90	20	11.6	6	1	27	37	20.7	12	3	52
09-Mar-90	103	43.7	6	0	109	183	97.2	6	0	189
24-Mar-90	77	24.4	23	5	105	77	40.4	4	0	81
07-Apr-90	80	18.3	37	3	120	163	62.1	18	8	189
20-Apr-90	60	12.9	17	4	81	83	69.0	10	2	95
05-May-90	90	17.5	49	4	143	40	15.6	16	20	76
18-May-90	57	14.5	76	7	140	13	6.6	37	9	59
01-Jun-90	63	20.6	130	6	199	77	29.2	40	58	175
14-Jun-90	73	25.0	157	23	253	107	40.1	121	105	333
28-Jun-90	77	17.0	75	9	161	203	56.4	44	29	276
13-Jul-90	77	15.2	96	21	194	143	40.2	46	11	200
25-Jul-90	167	35.7	17	7	191	53	15.4	3	0	56
09-Aug-90	243	113.9	10	1	254	120	55.2	0	0	120
14-Jan-91	-	-	13	16	-	-	-	0	0	-
04-Feb-91	-	-	7	10	-	-	-	6	0	-
19-Feb-91	-	-	8	0	-	-	-	20	0	-
05-Mar-91	-	-	4	1	-	-	-	12	0	-
19-Mar-91	-	-	2	2	-	-	-	6	0	-
30-Mar-91	46	-	4	4	54	60	-	1	0	61
13-Apr-91	57	12.3	3	0	60	90	37.8	5	1	96
27-Apr-91	47	10.9	11	1	59	33	15.0	5	0	38
10-May-91	97	20.2	4	3	104	73	39.2	4	0	77
25-May-91	57	12.0	9	0	66	33	12.2	4	0	37
08-Jun-91	33	9.4	5	0	38	23	8.6	6	0	29
22-Jun-91	43	11.9	5	3	51	40	17.1	14	0	54
09-Jul-91	37	9.8	15	3	55	47	15.1	40	1	88
22-Jul-91	60	12.8	12	2	74	87	29.0	9	0	96
04-Aug-91	117	23.8	42	1	160	130	48.7	23	0	153
01-Sep-91	17	5.8	13	1	31	110	27.2	72	1	183
18-Jan-92	90	23.2	10	0	100	110	18.8	13	3	126
18-Feb-92	33	10.9	17	1	51	137	23.7	39	0	176
12-Mar-92	300	213.6	35	0	335	240	143.3	22	1	263
16-Apr-92	60	17.0	8	5	73	27	7.0	11	2	40
22-May-92	33	9.7	7	0	40	180	40.8	17	1	198
19-Jun-92	103	21.2	17	0	120	223	48.3	17	6	246
18-Jul-92	79	21.8	10	1	90	106	21.8	4	0	110
15-Aug-92	40	9.9	10	5	55	87	18.8	8	0	95

Unidentified Small Dark Ardeids

Transects	std. err.	East-South Route	Eagle Bay Island	Total	SDA Total
2	-	-	-	2	24
4	-	7	0	11	93
2	-	3	0	5	52
0	-	7	0	7	58
0	-	0	0	0	156
106	-	0	90	196	446
260	94.2	0	0	260	548
275	73.8	4	0	279	395
320	97.8	39	8	367	638
277	171.0	2	0	279	885
287	96.0	3	0	290	355
410	130.8	0	0	410	533
83	42.6	2	0	85	130
420	99.3	6	0	426	494
500	170.8	13	1	514	877
1337	516.9	11	0	1348	1629
877	326.5	19	0	896	2012
430	195.5	11	0	441	907
97	29.6	21	0	118	570
33	17.8	44	0	77	385
73	22.0	1	0	74	178
317	166.5	1	0	318	492
180	61.0	2	0	182	261
360	151.9	6	0	366	664
600	199.5	4	0	604	790
723	244.2	3	3	729	1038
123	36.2	10	0	133	309
250	84.5	4	1	255	474
80	43.4	1	0	81	280
643	172.4	17	0	660	1034
947	279.9	3	0	950	1536
137	41.8	0	0	137	574
150	86.5	2	0	152	546
20	9.5	4	0	24	271
427	184.0	0	0	427	801
-	-	0	0	-	-
-	-	9	0	-	-
-	-	1	0	-	-
-	-	2	0	-	-
-	-	0	0	-	-
60	-	0	0	60	175
3	2.8	0	0	3	159
0	-	0	0	0	97
0	-	0	0	0	181
3	2.8	0	0	3	106
3	2.8	0	0	3	70
3	2.8	0	0	3	108
0	-	0	0	0	143
0	-	3	2	5	175
0	-	0	0	0	313
0	-	0	0	0	214
10	8.5	6	0	16	242
3	2.8	2	0	5	232
93	39.5	0	0	93	691
3	2.8	0	0	3	116
3	2.8	0	0	3	241
0	-	0	0	0	366
7	6.1	0	0	7	207
10	8.5	0	0	10	160

White Ibis

Survey Date	Transects	std. err.	East-South Route	Eagle Bay Island	Total
08-Aug-88	2220	-	-	-	2220
17-Sep-88	516	-	0	0	516
16-Oct-88	111	-	0	2	113
19-Nov-88	710	-	22	14	746
17-Dec-88	5096	-	5	15	5116
14-Jan-89	4264	-	75	157	4496
30-Jan-89	7193	1763.3	53	22	7268
11-Feb-89	6353	1938.0	244	797	7394
28-Feb-89	6030	1079.5	841	276	7147
15-Mar-89	3163	561.0	595	195	3953
27-Mar-89	3467	840.8	362	85	3914
10-Apr-89	1880	329.7	89	4	1973
25-Apr-89	757	189.8	74	6	837
09-May-89	1143	220.6	198	15	1356
22-May-89	5063	1131.1	232	2	5297
07-Jun-89	7473	1776.6	738	16	8227
19-Jun-89	14833	4469.9	501	83	15417
05-Jul-89	10220	2948.4	2124	59	12403
23-Jul-89	10793	2076.7	1888	128	12809
08-Aug-89	7537	1526.8	1537	40	9114
25-Jan-90	2953	453.1	514	77	3544
09-Feb-90	4123	633.4	398	171	4692
22-Feb-90	3940	611.4	338	298	4576
09-Mar-90	3593	588.5	371	365	4329
24-Mar-90	4150	802.8	86	126	4362
07-Apr-90	7960	2259.4	92	242	8294
20-Apr-90	3497	922.8	242	274	4013
05-May-90	3550	835.7	363	533	4446
18-May-90	4633	1044.3	367	504	5504
01-Jun-90	9063	2483.1	577	323	9963
14-Jun-90	27233	9146.1	918	529	28680
28-Jun-90	13897	4046.8	752	359	15008
13-Jul-90	5930	899.3	515	740	7185
25-Jul-90	637	201.7	38	445	1120
09-Aug-90	343	161.6	23	14	380
14-Jan-91	-	-	199	262	-
04-Feb-91	-	-	461	141	-
19-Feb-91	-	-	299	7	-
05-Mar-91	-	-	504	323	-
19-Mar-91	-	-	196	284	-
30-Mar-91	2818	-	218	102	3138
13-Apr-91	580	120.9	43	39	662
27-Apr-91	170	49.7	64	163	397
10-May-91	830	249.6	53	37	920
25-May-91	680	245.3	115	32	827
08-Jun-91	550	199.8	78	86	714
22-Jun-91	363	116.1	438	62	863
09-Jul-91	803	480.2	1896	607	3306
22-Jul-91	1087	595.9	803	358	2248
04-Aug-91	73	36.3	981	1	1055
01-Sep-91	0	-	116	2	118
18-Jan-92	847	275.8	288	29	1164
18-Feb-92	1378	426.3	560	24	1962
12-Mar-92	2227	662.4	187	35	2449
16-Apr-92	780	219.9	50	11	841
22-May-92	1087	277.4	62	7	1156
19-Jun-92	1293	275.1	1192	4	2489
18-Jul-92	13	8.0	441	1	455
15-Aug-92	43	25.9	79	0	122

Glossy Ibis

Survey Date	Transects	std. err.	East-South Route	Eagle Bay Island	Total
08-Aug-88	0	-	-	-	0
17-Sep-88	0	-	0	0	0
16-Oct-88	138	-	0	0	138
19-Nov-88	230	-	2	0	232
17-Dec-88	104	-	0	0	104
14-Jan-89	1102	-	94	0	1196
30-Jan-89	2866	1314.8	11	1	2878
11-Feb-89	2602	884.2	191	0	2793
28-Feb-89	377	121.0	90	19	486
15-Mar-89	2857	1617.7	170	0	3027
27-Mar-89	357	104.4	86	50	493
10-Apr-89	393	179.6	16	0	409
25-Apr-89	97	31.9	45	0	142
09-May-89	47	15.4	70	5	122
22-May-89	293	71.7	31	0	324
07-Jun-89	620	200.2	158	1	779
19-Jun-89	1357	821.5	415	1	1773
05-Jul-89	890	325.3	514	5	1409
23-Jul-89	1640	384.5	423	9	2072
08-Aug-89	577	186.4	288	30	895
25-Jan-90	1530	425.3	185	4	1719
09-Feb-90	2190	576.8	106	120	2416
22-Feb-90	1000	303.2	49	40	1089
09-Mar-90	1667	509.9	144	2	1813
24-Mar-90	710	188.4	132	91	933
07-Apr-90	720	259.6	1	71	792
20-Apr-90	683	301.6	62	181	926
05-May-90	1317	562.9	109	89	1515
18-May-90	400	182.6	198	249	847
01-Jun-90	1263	452.7	204	63	1530
14-Jun-90	1493	480.2	215	77	1785
28-Jun-90	2547	709.4	258	17	2822
13-Jul-90	1607	302.1	133	199	1939
25-Jul-90	223	66.8	11	162	396
09-Aug-90	47	13.1	0	1	48
14-Jan-91	-	-	12	75	-
04-Feb-91	-	-	17	0	-
19-Feb-91	-	-	45	0	-
05-Mar-91	-	-	72	80	-
19-Mar-91	-	-	1	0	-
30-Mar-91	549	-	112	56	717
13-Apr-91	190	52.2	6	1	197
27-Apr-91	70	25.1	14	4	88
10-May-91	183	86.8	0	0	183
25-May-91	77	26.7	0	0	77
08-Jun-91	30	11.4	20	0	50
22-Jun-91	67	55.7	185	0	252
09-Jul-91	47	31.6	330	35	412
22-Jul-91	50	41.8	276	1	327
04-Aug-91	0	-	513	0	513
01-Sep-91	0	-	32	0	32
18-Jan-92	90	32.6	147	0	237
18-Feb-92	377	230.4	108	0	485
12-Mar-92	593	217.7	70	0	663
16-Apr-92	277	116.2	99	1	377
22-May-92	10	6.1	8	0	18
19-Jun-92	197	67.0	291	1	489
18-Jul-92	0	-	6	0	6
15-Aug-92	0	-	3	0	3

Wood Stork

Survey Date	Transects	std. err.	East-South Route	Eagle Bay Island	Total
08-Aug-88	0	-	-	-	0
17-Sep-88	0	-	0	0	0
16-Oct-88	0	-	0	0	0
19-Nov-88	0	-	1	0	1
17-Dec-88	0	-	71	0	71
14-Jan-89	110	-	0	0	110
30-Jan-89	77	57.9	0	0	77
11-Feb-89	10	8.3	7	0	17
28-Feb-89	323	147.6	0	0	323
15-Mar-89	513	352.2	0	2	515
27-Mar-89	253	196.4	1	3	257
10-Apr-89	7	5.6	0	0	7
25-Apr-89	0	-	0	0	0
09-May-89	0	-	0	0	0
22-May-89	43	36.6	0	1	44
07-Jun-89	240	117.6	13	0	253
19-Jun-89	277	163.3	17	0	294
05-Jul-89	33	14.5	7	0	40
23-Jul-89	23	17.2	0	0	23
08-Aug-89	90	70.7	1	0	91
25-Jan-90	0	-	4	0	4
09-Feb-90	0	-	0	0	0
22-Feb-90	0	-	1	0	1
09-Mar-90	0	-	0	0	0
24-Mar-90	0	-	0	0	0
07-Apr-90	0	-	1	0	1
20-Apr-90	0	-	16	0	16
05-May-90	3	2.9	2	0	5
18-May-90	0	-	0	0	0
01-Jun-90	130	67.7	56	4	190
14-Jun-90	600	290.1	117	1	718
28-Jun-90	200	93.2	194	12	406
13-Jul-90	3	2.8	3	0	6
25-Jul-90	0	-	1	0	1
09-Aug-90	0	-	0	0	0
14-Jan-91	-	-	0	0	-
04-Feb-91	-	-	0	0	-
19-Feb-91	-	-	1	0	-
05-Mar-91	-	-	0	0	-
19-Mar-91	-	-	0	0	-
30-Mar-91	0	-	0	0	0
13-Apr-91	0	-	0	0	0
27-Apr-91	0	-	0	0	0
10-May-91	0	-	1	0	1
25-May-91	0	-	0	0	0
08-Jun-91	0	-	0	0	0
22-Jun-91	0	-	0	0	0
09-Jul-91	0	-	0	0	0
22-Jul-91	0	-	0	0	0
04-Aug-91	0	-	0	0	0
01-Sep-91	0	-	0	0	0
18-Jan-92	0	-	0	0	0
18-Feb-92	0	-	0	0	0
12-Mar-92	0	-	0	2	2
16-Apr-92	0	-	0	0	0
22-May-92	0	-	0	0	0
19-Jun-92	0	-	0	0	0
18-Jul-92	0	-	0	0	0
15-Aug-92	0	-	0	0	0

Roseate Spoonbill

Survey Date	Transects	std. err.	East-South Route	Eagle Bay Island	Total
08-Aug-88	0	-	-	-	0
17-Sep-88	0	-	0	0	0
16-Oct-88	0	-	0	0	0
19-Nov-88	0	-	0	0	0
17-Dec-88	0	-	0	0	0
14-Jan-89	0	-	0	0	0
30-Jan-89	0	-	0	0	0
11-Feb-89	0	-	0	0	0
28-Feb-89	0	-	0	0	0
15-Mar-89	0	-	0	0	0
27-Mar-89	3	2.8	0	0	3
10-Apr-89	0	-	0	0	0
25-Apr-89	0	-	0	0	0
09-May-89	0	-	0	0	0
22-May-89	0	-	27	0	27
07-Jun-89	0	-	8	0	8
19-Jun-89	0	-	53	0	53
05-Jul-89	0	-	42	0	42
23-Jul-89	10	8.4	37	0	47
08-Aug-89	3	2.8	12	0	15
25-Jan-90	0	-	0	0	0
09-Feb-90	0	-	0	0	0
22-Feb-90	0	-	0	0	0
09-Mar-90	0	-	0	0	0
24-Mar-90	0	-	0	0	0
07-Apr-90	0	-	4	0	4
20-Apr-90	47	36.4	5	0	52
05-May-90	7	5.6	11	0	18
18-May-90	0	-	6	0	6
01-Jun-90	20	14.1	21	0	41
14-Jun-90	53	44.5	68	4	125
28-Jun-90	13	6.9	71	13	97
13-Jul-90	83	68.9	29	2	114
25-Jul-90	0	-	0	0	0
09-Aug-90	0	-	0	0	0
14-Jan-91	-	-	0	0	-
04-Feb-91	-	-	6	0	-
19-Feb-91	-	-	0	0	-
05-Mar-91	-	-	0	0	-
19-Mar-91	-	-	1	0	-
30-Mar-91	0	-	0	0	0
13-Apr-91	0	-	0	0	0
27-Apr-91	0	-	0	0	0
10-May-91	0	-	0	0	0
25-May-91	0	-	0	0	0
08-Jun-91	0	-	0	0	0
22-Jun-91	0	-	0	0	0
09-Jul-91	0	-	0	0	0
22-Jul-91	0	-	0	0	0
04-Aug-91	0	-	0	0	0
01-Sep-91	0	-	0	0	0
18-Jan-92	23	19.5	0	0	23
18-Feb-92	0	-	0	0	0
12-Mar-92	0	-	0	0	0
16-Apr-92	0	-	0	0	0
22-May-92	0	-	0	0	0
19-Jun-92	0	-	0	0	0
18-Jul-92	0	-	0	0	0
15-Aug-92	0	-	0	0	0

Combined-Species Totals

Survey Date	Transects	East-South Route	Eagle Bay Island	Total
08-Aug-88	3334	-	-	3334
17-Sep-88	2772	72	23	2867
16-Oct-88	2794	171	27	2992
19-Nov-88	3329	176	40	3545
17-Dec-88	7865	244	69	8178
14-Jan-89	8958	382	581	9921
30-Jan-89	13666	380	28	14074
11-Feb-89	12578	780	1064	14422
28-Feb-89	12400	1662	336	14398
15-Mar-89	12657	1333	223	14213
27-Mar-89	9601	755	197	10553
10-Apr-89	11607	376	40	12023
25-Apr-89	4103	285	38	4426
09-May-89	5326	616	87	6029
22-May-89	14765	773	76	15614
07-Jun-89	18566	1763	70	20399
19-Jun-89	33621	2255	146	36022
05-Jul-89	19364	3345	134	22843
23-Jul-89	17213	3309	215	20737
08-Aug-89	14726	2853	168	17747
25-Jan-90	6099	1170	128	7397
09-Feb-90	8931	999	376	10306
22-Feb-90	6777	951	411	8139
09-Mar-90	7957	854	418	9229
24-Mar-90	8573	609	268	9450
07-Apr-90	13797	758	456	15011
20-Apr-90	7096	1208	545	8849
05-May-90	9477	1544	813	11834
18-May-90	10430	1778	961	13169
01-Jun-90	19586	2098	702	22386
14-Jun-90	46833	3116	1099	51048
28-Jun-90	21985	3264	888	26137
13-Jul-90	12667	1585	1228	15480
25-Jul-90	3783	399	823	5005
09-Aug-90	3426	239	116	3781
14-Jan-91	-	440	482	-
04-Feb-91	-	997	283	-
19-Feb-91	-	635	107	-
05-Mar-91	-	849	577	-
19-Mar-91	-	373	359	-
30-Mar-91	5234	637	253	6124
13-Apr-91	2084	185	83	2352
27-Apr-91	1494	233	207	1934
10-May-91	2044	214	87	2345
25-May-91	2466	220	148	2834
08-Jun-91	1663	262	217	2142
22-Jun-91	1139	769	152	2060
09-Jul-91	1623	2483	746	4852
22-Jul-91	2064	1320	503	3887
04-Aug-91	1097	2057	176	3330
01-Sep-91	1953	624	124	2701
18-Jan-92	5124	1404	156	6684
18-Feb-92	5432	1918	141	7491
12-Mar-92	7780	1142	143	9065
16-Apr-92	4204	489	99	4792
22-May-92	3413	407	112	3932
19-Jun-92	5159	1989	143	7291
18-Jul-92	708	526	12	1246
15-Aug-92	2543	196	115	2854

APPENDIX B
RATE-COEFFICIENT CALCULATIONS
FOR GREAT EGRET POPULATION MODEL

Averages Used to Calculate Rate Coefficients

Weekly solar insolation (SUN) = 28,150 kcal m^{-2} $week^{-1}$ or 56.30% of arbitrary maximum 50,000 (data from Browder 1976 collected at the Belle Glade Agricultural Experiment Station, Belle Glade, Florida)

Weekly-mean minimum daily air temperature (MINT) = 16.7 °C (data provided by Belle Glade Agricultural Experiment Station)

Surface-water area = 417.3E6 m^2 (WAREA) or 85.34% (WA) of 489 square-kilometer transect-survey grid cells (data derived from OKEEHYDRO model; Richardson and Hamouda 1994)

Prey biomass density (DENS) = 18.2 g m^{-2} (derived from field data summarized in part in McIvor and Smith 1992, from data provided by J. H. Chick and C. C. McIvor--see Chick and McIvor 1994, and from data provided in Bull et al. 1992)

Total prey biomass (BP) = 18.2 g m^{-2} x 417.3E6 m^2 x 1.5 = 1.1392E10 g

Number of foraging Great Egrets (NB) = 2,200 (derived from survey data; Chapter 2)

Ratio of non-Great Egrets to Great Egrets = 3.17 (ratio calculated from survey data; Chapter 2)

Average mass of adult Great Egret = 1,000g (rough approximation based on unpublished field data and data in Palmer 1962)

Average adult Great Egret food requirement = 181 g day^{-1} (based on the regression equation provided in Kushlan 1978a)

Average Great Egret nestling food requirement = 117 g day^{-1} (based on data in Mock et al. 1987 and the assumption that nestling requirements equal adult needs by 30 days)

Average egg mass = 27.4 g (based on unpublished hatch-day measurements of Great Egret nestlings)

Average food requirements for Great Egret population
= (2,200 adults * 181 g $bird^{-1}$ day^{-1} * 7 days $week^{-1}$) + (600 nestlings * 117 g $bird^{-1}$ day^{-1} * 7 days $week^{-1}$) + (100 eggs * 27.4 g egg^{-1})
= 3.2815E6 g $week^{-1}$

Relative energy needs of non-Great Egrets = 0.83 (rough estimate based on observed relative representation of species of different mass in population--Chapter 2--and the regression equation provided in Kushlan 1978a)

Great Egret mean clutch size = 2.9 eggs (Chapter 4)

Great Egret % eggs hatched = 53% (derived from data discussed in Chapter 4)

Great Egret % hatched-eggs fledged = 58% (derived from data discussed in Chapter 4)

Great Egret first-year mortality = 76% (Kahl 1963)

Great Egret mortality in subsequent years = 26% (Kahl 1963)

Rate Coefficient Calculations

JR = SUN / (1 + K0 * BP * WA)

K0 = J0 / (BP * JR * WA)
= (0.1 * SUN) / (0.9 * SUN * BP * WA)
= 0.1111 / (1.1392E10 * 0.8534)
= 1.1428E-11 ($kcal^{-1}$)

Average JR = 0.563 / (1 + 1.1428E-11 * 1.1392E10 * 0.8534)
= 0.5067 kcal m^{-2} $week^{-1}$

K1 = J1 / (JR * BP * (1 - EXP(-4 * WA)))
= (0.25 * 1.1392E10 * 7 days) / (0.5067 * 1.1392E10 * (1 - EXP(-4 * 0.8534)))
= 3.5713 ($kcal^{-1}$) (increased by factor of 3 during simulation)

K2 = J2 / (BP * BP)
= 0.1 * BP / (BP * BP)
= 0.1 / 1.1392E10
= 8.7787E-13 (g^{-1} $week^{-1}$)

K3 = J3 * WA / (BP * BP)
= 0.2 * BP * WA / (BP * BP)
= 0.2 * 0.8534 / 1.1392E10
= 1.4982E-11 (m^2 g^{-1} $week^{-1}$)

K4 = J4 * WA / BP
= 0.05 * BP * WA / BP
= 0.05 * 0.8534
= 0.0427 (m^2 $week^{-1}$)

K5 = J5 / (LOG(BP / WA) * (NB + NN + NENEW) * (1 / (1 + 600 * EXP(-0.55 * MINT))) * ((0.03-DR)*33.333))
= 3.2815E6 / (LOG(1.1392E10 / 0.8534) * (2,200 + 600 + 100) * (1 / (1+600*EXP (-0.55*16.7))) * ((0.03-0)*33.333))
= 118.63 (m^2 $bird^{-1}$ or egg^{-1} $°C^{-1}$ $week^{-1}$)
(adjusted during simulation to 0.88 * 118.63)

B6 = 3.17 non-GE:GE * 0.83 energy requirement reduction factor
= 2.6311

K7 = J7 / NB
= 0.26 * NB mortality per year / 52 weeks per year / NB
= 0.005 ($week^{-1}$)

K8 = 1 ($week^{-1}$) (adjusted to 1.4 during simulation)

K9 = J9 / (NBRNEW * CL)
= NBRNEW / 2 * CL / (NBRNEW * CL)
= 0.5 (eggs per breeding bird)

K10 = J10 * PFA / NE
= (0.47 NE hatching failure / 4 weeks in incubation period) * 1.3 / NE
= 0.1528 ($week^{-1}$)

K11 = J11 / (NE * PFA * HATSW)
= (0.53 NE hatching success / 4 weeks in incubation period) / (NE * 1.3 * 1)
= 0.1019 ($week^{-1}$)

K12 = J12 * PFA / NN
= (0.42 NN fledging failure / 9 weeks in nestling period) * 1.8 / NN
= 0.0840 ($week^{-1}$)

K13 = J13 / (NN * PFA * FLGSW)
= (0.58 NN fledging success / 9 weeks in nestling period) / (NN * 1.8 * 1)
= 0.0358 ($week^{-1}$)

K14 = J14 / NF1
= (0.76 NF1 mortality per year / 52 weeks per year) / NF1
= 0.0146 ($week^{-1}$)

K15 = 1 ($year^{-1}$)

K16 = J16 / NF2
= ((0.76 + 0.26) / 2 NF2 mortality per year / 52 weeks per year) / NF2
= 0.0098 ($week^{-1}$)

K17 = J18 / NF2
= 0.6 * NF2 / NF2
= 0.6 ($year^{-1}$)

K18 = J18 / NF2
= 0.4 * NF2 / NF2
= 0.4 ($year^{-1}$)

K19 = J19 / NF3
= (0.26 NF3 mortality per year / 52 weeks per year) / NF3
= 0.005 ($week^{-1}$)

K20 = 1 ($year^{-1}$)

K21 = 1 ($week^{-1}$)

K22 = 600 ($week^{-1}$) (maximum rate adjusted during simulation)

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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